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Seasonal Effects of Defoliation on Montane Rough Fescue (Festuca campestris Rydb.)

by

Leslie Erica McInenly ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of *Master of Science*

in

Environmental Biology and Ecology

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Dr. Evelyn Merrill

Dr. Noorallah Juma

Dr. James Cahill

Date Thesis Approved: Sept 12, 2003

ABSTRACT

Montane rough fescue (*Festuca campestris* Rydb.) grasslands were historically grazed in winter, but changes in migratory behavior of elk (*Cervus elaphus*) may lead to year-long grazing. I describe spatio-temporal patterns in nutrient return on a fescue grassland at the Ya-Ha-Tinda ranch, responses of grassland plants and soils to seasonal defoliation, and fescue plant responses to nitrogen-form and defoliation. Elk pellet group distribution shifted seasonally and was associated with site productivity, rough fescue, topography, and vegetation cover. In a 2-year field experiment, aboveground carbon and nitrogen pools at the community level responded to changes in seasonal defoliation while root biomass and soil N did not change. A greenhouse experiment showed that declines in rough fescue under high nitrogen availability and defoliation result from decreased tillering and root growth, not increased mortality. I discuss my research results in light of changing migratory patterns of elk and the sustainability of elk-fescue grasslands.

For Paul

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CHAPTER 1

INTRODUCTION

1.1. BACKGROUND

Fescue grasslands are some of the most threatened communities in the Canadian Prairie Provinces (Vujnovic 1998) and have recently been described as an endangered ecosystem by Environment Canada (Trottier 2002). Concern about their loss due to development, woodland encroachment, exotic species and overgrazing has increased because only 5% of the grasslands remain in pre-settlement condition (Vujnovic 1998). The majority of fescue grasslands are in the foothills region east of the Canadian Rocky Mountains (Dormaar and Willms 1990). These grasslands are some of the most productive among the prairie grasslands in North America (Willms et al. 1996), providing valuable forage for native and non-native ungulates (Stout et al. 1981, and Willms 1987).

The rough fescue complex in Canada is found on highly productive soils and spreads out over the Prairie Provinces from central Alberta into southwestern Manitoba (Willms 1988, Dormaar and Willms 1990, Willms et al. 1996). Three rough fescue species define these grasslands over different geographical ranges. Plains rough fescue (*Festuca hallii*) is found in dry, subhumid parkland regions usually below 1000 m (Pavlick and Looman 1984, Naethe and Chanasyk 1996, and King et al. 1998). Alpine rough fescue (*F. altaica*) is a montane species predominantly found in Alaska and the Yukon Territory. Mountain rough fescue (*F. campestris*) is mainly found in the foothills region between 1000 and 1700 m (Pavlick and Looman 1984 and Willms et al. 1996). The foothills experience a more moderate, subhumid climate, mediated by warm Chinook winds contributing to an annual temperature of 5°C with mean July temperature of 18°C and January temperature of 10°C (Naethe et al. 1991 and Naethe and Chanasyk 1996). The growing season for *F. campestris* experiences moister, cooler springs and drier summers than *F. altaica* or *F. hallii*, leading to earlier flowering. Mountain rough fescue experiences optimum growth at 12°C (Hill et al. 1997).

The Parks Canada Ya Ha Tinda Ranch, in the Rocky Mountain foothills west of Sundre, Alberta exhibits an azonal (Looman 1969) mountain rough fescue grassland that covers approximately 3000 ha. Today, the ranch is considered one of the most important winter ranges for elk (*Cervus elaphus*) in Alberta (Alberta Forestry 1986 and Morgantini 1995). Increasing levels of growing season (spring and summer) grazing by elk on the Ya Ha Tinda (Hebblewhite 2002) has caused concern for the long-term sustainability of the fescue grasslands on the ranch. In addition, Parks Canada is currently evaluating the potential for bison (*Bison bison*) reintroduction in the upper Red Deer valley, including the Ya Ha Tinda Ranch (Shury 2000).

Prior to the 1900s, use of the ranch grasslands by native ungulates is not clear. There are accounts that bison and elk migrated into the foothills and used the rough fescue communities as winter range (Dwnyer 1969 and Morgan 1980). However, past patterns of bison use in the east slopes are in debate. One scenario suggests that bison were migratory using the foothill grasslands only in winter (Johnston and MacDonald 1967); the second is that bison used the foothills on a year-round basis (see Langemann 2000). No bison exist in this area today.

Since the 1900s, the Ya Ha Tinda rough fescue grasslands have provided rich grazing opportunities for domestic as well as native ungulates (Alberta Forestry 1986, Benn et al. 1988). The first ranching operation on the Ya Ha Tinda was a grazing lease issued to the Brewster brothers by the federal government between 1907 and 1917 (Morgantini 1995). During the early ranch years, the ranch was within the Rocky Mountain Park boundary. Park boundary revisions between 1911 and 1917 excluded, and then re-included the Ya Ha Tinda Ranch in the Park. With the incorporation of the Ya Ha Tinda back into the National Park, the ranch became Warden District Headquarters in 1917 (Morgantini 1995). The National Parks Act excluded the Ya Ha Tinda from the newly created Banff National Park in 1930; however, Banff park wardens continued to maintain the ranch (McGillis 1977). While legal ownership status of the ranch has been varied, park officials have administered the ranch for over 80 years.

The Brewster's ranch grazed up to 300 horses and a smaller number of cattle (McGillis 1977). In 1917, Banff wardens started using the ranch for over-wintering approximately 65 horses (McGillis 1977). For the past forty years, Parks Canada has over-wintered approximately 170-200 horses at the Ya Ha Tinda (McGillis 1977 and Morgantini 1995). Currently, summer horse grazing is restricted to approximately 30 horses, primarily breeding mares, yearlings and foals. Because of concerns about the impact of early-season grazing on the fescue grasslands, horses are fenced in a pasture mid-March and supplemented with weedseed-free hay and oats (M. Nylund, pers. comm).

According to Morgantini and Hudson (1989), the current elk population in the Ya Ha Tinda likely originated from animals reintroduced (from Wyoming) into the Bow valley between 1917 and 1920 and which subsequently colonized surrounding valleys. Although old antlers were found in the early 1900s (McGillis 1977), earliest recorded observations of elk on the Ya Ha Tinda Ranch date from the 1930s (Morgantini 1988).

By 1943, nearly 60 elk wintered in the ranch area (McGillis 1977). Based on provincial game surveys conducted between 1973 and 2000, a fluctuating, but positive, trend in over-wintering elk occurred over the last 30 years (AB-SRD Files, Rocky Mountain House). In the past decade, winter surveys conducted by Alberta Environment documented over 2000 elk in the Ya Ha Tinda area (AB-SRD Files, Rocky Mountain House).

The proportion of the migratory elk population summering on the Ya Ha Tinda Ranch also appears to be increasing. In 1981 and 1982, research on the migratory elk indicated only 25-50 (2-8%) elk remained on the ranch during the summer (Morgantini and Hudson 1989 and Hebblewhite 2002), whereas in summers 2000 and 2001, maximum ground counts (i.e. minimum true count) by ranch staff between June and August ranged from 150-200 (16-24%) elk and the maximum count in summer 2002 was 350 (33%) (Hebblewhite 2002). Although elk populations often have migratory and resident components (Morgantini 1988 and Woods 1991), the cause for the recent increase in Ya Ha Tinda summering elk number is unknown. One hypothesis is that elk are remaining on the ranch to avoid predation, similar to what is suspected to have occurred with habituated elk in the townsites of Jasper and Banff national parks (White et al. 1998).

The increase in elk numbers on the ranch has raised concerns about possible degradation of the fescue grassland since the 1950s (Flook 1957, AGRA Earth and Environmental Ltd. 1998). In 1958, the Canadian Wildlife Service established three clusters of Parker Three-Step transects to monitor range condition (Flook 1960). These clusters were re-sampled by Canadian Wildlife Service in 1962 and 1973, but received only minor analyses (McGillis 1977). Most of the fescue grassland on the Ya Ha Tinda was not excessively utilized in 1974, except in local areas, such as along Scalp Creek where fescue abundance and productivity was high and grazing off-take (82%) was considered at a level, which would cause "inevitable" deterioration if continued (McGillis 1977). Nonetheless, based upon the sensitivity of rough fescue to early spring grazing, McGillis (1977) recommended either moving horses off the ranch before the growing season or corralling horses in spring and providing supplemental hay. Range studies in 1988 indicated range productivity was "severely reduced" as a result of both grazing in late spring and a large number (50-80/m^2) of grasshoppers present during the growing season (Seel and Wiebe 1988). Recently, fescue communities rated as primary range (i.e. high productivity and high percent rough fescue) for elk and domestic use on the Ya Ha Tinda were reported to have production levels below that expected for the soil types, decreased abundance of rough fescue plants, and increased levels of Fringed brome (*Bromus ciliatus*), June grass (*Koeleria macrantha*), and sedges (*Carex spp.*) (AGRA Earth and Environmental Ltd. 1998). In the same study, fescue grasslands on the west side of the Ya Ha Tinda, which were "used extensively" by horses, were found to be in an earlier successional stage than communities in similar sites while grazing resulted in decreases in rough fescue (no rough fescue was found during the inventory) and increases in sedges and June grass (AGRA Earth and Environmental Ltd. 1998).

Most studies of grazing on mountain rough fescue communities have focused on the plant community responses to cattle grazing, and little is known of impacts from native herbivores. Shifts in traditional season grazing patterns of large herbivores could have implications for long-term sustainability of fescue grasslands. If bison were migratory in the Banff region and left before spring green-up, they may have used the foothills community only for winter grazing (Moss and Campbell 1947, Johnston and McDonald 1967, and Dormaar and Willms 1990). If so, the ecological impacts of spatially and temporally distributed grazing may be quite dissimilar from the grassland responses observed at fescue prairies to date (Willoughby 1992). Conversely, if current research provides archeological evidence of resident bison in the Rocky Mountain foothills (Langemann 2000), grazing may have resembled a year-round regime.

1.2. STUDY OBJECTIVES

This project addressed 3 major questions:

1) Where does grazing occur on the Ya Ha Tinda Ranch and how does it change seasonally?
2) How does seasonal clipping affect soil nitrogen cycling, rough fescue growth and survival, and grassland community composition and productivity?
3) How does high inputs of nitrogen fecal excreta in grazed systems influence recuperation of rough fescue from defoliation? In particular, does rough fescue change root morphology and demography as a result of defoliation and/or mineral N form?

In chapter 2, I describe the spatial and temporal distribution of elk use of the Ya Ha Tinda Ranch in 2001- 2002, and identify environmental factors associated with areas of high elk use. In Chapter 3, I report the short-term responses of plants and soils within fescue communities to a 2-year defoliation experiment designed to mimic current levels of seasonal defoliation on the Ya Ha Tinda Ranch. In Chapter 4, I describe a greenhouse experiment that addressed the effects of mineral nitrogen form and clipping on plant regrowth and the associated on changes in root morphology and demography.

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CHAPTER 2

SEASONAL GRAZING PATTERNS OF UNGULATE USE ON YA HA TINDA RANCH

2.1 INTRODUCTION

The relationships among plants, animals, and abiotic factors, and the spatial patterns they create, are increasingly recognized for their important role in ecosystem processes (Gross et al. 1995, Tilman and Karieva 1997, Stohlgren et al. 1999, Turner and Carpenter 1999, Broughton and Gross 2000, Augustine and Frank 2001, Barthram et al. 2002). In grazed ecosystems, biotic and abiotic factors, such as forage quality and distance to water, influence herbivore distribution (Senft et al. 1985, Bailey et al. 1996, Brock and Owensby 2000). Conversely, herbivores have been reported to promote plant and nutrient heterogeneity, at various spatial scales, via urine and fecal deposition (Day and Detling 1990, Hobbs 1996, Frank and Evans 1997, Hamilton et al. 1998), visitation of preferred plants or locations such as vegetation edges (Senft et al. 1987, Wallace et al 1995, Hobbs 1996, Frank and Groffman 1998, Palmer and Hester 2000, Steinauer and Collins 2001), or migration across landscapes (McNaughton 1985, Archer and Smeins 1991, Frank et al. 1998, Augustine and Frank 2001). Often herbivore distribution has resulted in limited plant distribution, such as willow (*Salix* spp) within Rocky Mountain National Park (Peinetti et al. 2002) and aspen (*Populus tremuloides*) in the Canadian Rockies (White 2001).

Fescue grasslands are some of the most threatened communities in the Canadian Prairie Provinces (Vujnovic 1998). Concern about their loss due to development, woodland encroachment, exotic species, and overgrazing has increased because only 5% of the grasslands remain in historical condition (Vujnovic 1998). The majority of fescue grasslands are in the foothills region east of the Canadian Rocky Mountains (Dormaar and Willms 1990). These grasslands are some of the most productive among the prairie grasslands in North America (Willms et al. 1996), providing valuable forage for native and non-native ungulates (Stout et al. 1981, Willms et al. 1986). The Parks Canada Ya Ha Tinda Ranch in the Rocky Mountain foothills west of Sundre, Alberta exhibits an azonal mountain rough fescue (*Festuca campestris* Rydb) grassland (Looman 1969). Today the ranch is considered one of the most important winter ranges for elk (*Cervus elaphus*) in Alberta (Alberta Forestry 1986, Morgantini 1995). Prior to the 1900's, use of the Ya Ha Tinda fescue grasslands by native ungulates is not clear. There are accounts that bison and elk migrated into the foothills and used the rough fescue communities as winter range (Dwnyer 1969, Morgan 1980). Since the 1900's, the ranch grasslands have provided rich grazing opportunities for domestic as well as native ungulates (Alberta Forestry 1986, Benn et al. 1988). But a fluctuating, yet positive trend in over-wintering elk since the 1940's has raised issues about possible degradation of the fescue grassland due to heavy winter and spring grazing (Flook 1957, AGRA Earth and Environmental Ltd. 1998). In recent years, winter surveys conducted by Alberta Environment have documented approximately 1000 elk in the Ya Ha Tinda area (Alberta Sustainable Resource Development Files, Rocky Mountain House). In addition, an increasing number of elk are summering on the Ya Ha Tinda Ranch (Hebblewhite and Morgantin 2003). Although elk populations often have migratory and resident components (Morgantini 1988, Woods 1991), the cause for the recent increase in Ya Ha Tinda summering elk number is unknown. One hypothesis is that elk are remaining on the ranch to avoid predation, similar to what is suspected to be occurring with habituated elk in the town sites of Jasper and Banff national parks (White et al. 1998).

In addition to high grazing pressure from elk, Parks Canada has over-wintered approximately 170-200 horses at the Ya Ha Tinda each year for the past forty years (McGillis 1977, Morgantini 1995). Under Parks Canada jurisdiction, summer horse grazing has been restricted to approximately 30 horses, primarily breeding mares, yearlings and foals. Studies of wild horses and elk in the outer foothills of Alberta have shown that both species prefer dry grassland habitat and south facing slopes in winter and spring and that there is as much as 50% diet overlap, primarily resulting from selection of grasses including hairy wild-rye (*Elymus innovatus*), fescues, and sedges (*Carex* spp.) (Salter and Hudson 1980). While there was little support for behavioral interference, spatial and dietary overlap indicated a potential for competition, particularly for fescue species (Salter and Hudson 1980).

The combined heavy winter and increasing summer use by elk, along with continued horse use have caused concern for the long-term sustainability of the fescue grasslands on the ranch. In addition, Parks Canada is currently evaluating the potential for bison reintroduction in the upper Red Deer valley, including the Ya Ha Tinda Ranch (Shury 2000, White et al. 2001). As a result, I investigated the use patterns of native and domestic herbivores at the Parks Canada Ya Ha Tinda Ranch to better understand the spatial and temporal patterns of elk distribution and their potential grazing pressures in the fescue grasslands on the Ya Ha Tinda Ranch. My specific objectives were to quantify the elk distributions and to determine what habitat variables were associated with seasonal distribution across the grassland. I did not quantify factors associated with horse distribution on the ranch because horses were constrained by fences. I hypothesized that the broad-scale patterns in elk pellet distribution within the grasslands of the Ya Ha Tinda Ranch were related to (1) overall plant abundance, and in particular to rough fescue because of its high value as a forage (Bezeau and Johnston 1962), (2) local topography because it may mitigate thermal or snow conditions (Millspaugh et al. 1998) as well as predation risk (Kunkel and Pletscher 2001), (3) abundance of horse pellet groups because elk may avoid horses (Salter and Hudson 1980), (4) distance to human activity and cover because elk are known to be sensitive to human disturbance and hiding cover can mitigate this effect (Geist 1982), and (5) distance to water. Identifying current levels of use by elk and factors associated with their use is important for assessing future changes in elk populations as well as understanding how future management decisions at the ranch related to grazing horses and reintroducing bison may influence grazing pressure on the fescue grasslands of the Ya Ha Tinda Ranch.

2.2 METHODS

2.2.1 Study site

The Ya Ha Tinda Ranch is located approximately 5 km east of the Banff National Park boundary along the Red Deer River Valley in Alberta. Central coordinates of the ranch are 51° 45' latitude and 115° 35' longitude. Average elevation of Ya Ha Tinda is about 1550 m, consisting of dry, rolling grassland and forest surrounded by high mountains (Morgantini 1995). The climate is Cordilleran with westerly winds that, in addition to low precipitation, keep the grasslands mostly snow-free in the winter (Benn et al. 1988). Geologic parent material consists of glacial till (Seel and Wiebe 1988) and colluvial veneers (AGRA Earth and Environmental 1998). Grassland soils consist primarily of Orthic Black and Eluviated Black Chernozems, Orthic Melanic Brunisols, Orthic Regosols, and Orthic Grey Luvisols (McGillis 1977, AGRA Earth and Environmental 1998).

The ranch is approximately 4400 ha and consists of grassland, shrubland, and forest. The grasslands, which cover nearly 30% of the ranch, have been described as a variant of the *Festuco-Stipetum richardsoni* association (Looman 1969). Common grasses include rough fescue, rocky mountain fescue (*F. saximontana*), June grass (*Koeleria macrantha*), Hooker's oat grass (*Helicotrichon hookeri*), slender wheat grass (*Agropyron trachycaulum*), hairy wild rye, Fringed brome (*Bromus ciliatus*), and Smooth brome (*Bromus inermis pumpellianus*) (AGRA Earth and Environmental 1998). Forests consist primarily of lodgepole pine (*Pinus contorta*), trembling aspen (*Populus tremuloides*), and white spruce (*Picea glauca*), while common shrubs include bog birch (*Betula glandulosa*), shrubby cinquefoil (*Potentilla fruticosa*) and willow (McGillis 1977).

2.2.2 Pellet count surveys

Twice a year, pellet surveys were conducted across the non-forested portions of the Ya Ha Tinda Ranch to map relative ungulate distribution (Table 2.1). The surveyed portion of the ranch was determined by digitizing a large polygon from a 15 September 1998 TM satellite image (excluding continuous forested portions of the ranch), and by field verification of non-forest classification based upon a canopy cover of less than 60% as measured by a spherical densiometer. Spring pellet group counts were conducted during the first two weeks of May and represented grazing on the ranch during the dormant season (winter). Fall surveys were conducted during the last two weeks of

Table 2.1. Dates, number of survey participants, and number of 25-m^2 and 100-m^2 plots sampled on grassland pellet group counts conducted in 2000-2002 across the Ya Ha Tinda in Central Alberta.

Survey	Date	Person Days	No. Plots (25 m^2)	No. Plots (100 m^2)
Summer 2000	23-30 Sept	14	276	0
Winter 2001	4-10 May	14	271	53
Summer 2001	19-25 Sept	14.5	277	277
Winter 2002	4-14 May	15	273	29

September and represent grazing on the ranch during the growing season (summer) prior to the return of migratory elk (Hebblewhite 2002). Pellet counts were conducted at 271 to 277 points on a systematic grid of sampling sites located at 250-m intervals placed across the grasslands on Ya Ha Tinda using a random starting point on a map (Fig. 2.1).

During each survey, sample sites were located with a Garmin 12XL global position system (GPS). Number of elk, deer (*Odocoileus hemionus* and *O. virginianus*)/sheep (*Ovis canadensis*), moose (*Alces alces*) and horse pellet groups were counted within each 25-m^2 plot. Deer, sheep, and moose pellets were encountered so rarely that they were not included in analyses. A pellet group was defined as at least 8 pellets and distribution of the pellets was taken into account in distinguishing between groups (but see Neff 1968). If greater than 50% of the pellet group was within the plot border, it was included in the count. Because plots were not permanently marked, pellets were not cleared before survey seasons. To indicate the age of the pellet groups, pellet groups were recorded as black, gray or white for elk, deer, sheep, and moose or dark and light for horses in all surveys except in fall 2000 when only black pellets were recorded. Black pellets were considered to have been deposited since the last sampling period. To examine the potential influence of plot size on pellet counts, pellet groups also were counted within 100-m^2 plot at a sub-sample of survey plots in spring 2001 and spring 2002 and in all plots in fall 2001. Counts in the 100-m^2 plots were obtained by searching the smaller plot and then a 75-m^2 ring around it.

Environmental variables

Variables that were visually recorded in the field at each sample plot included percent canopy cover of standing plant material (live and dead) and percent basal cover

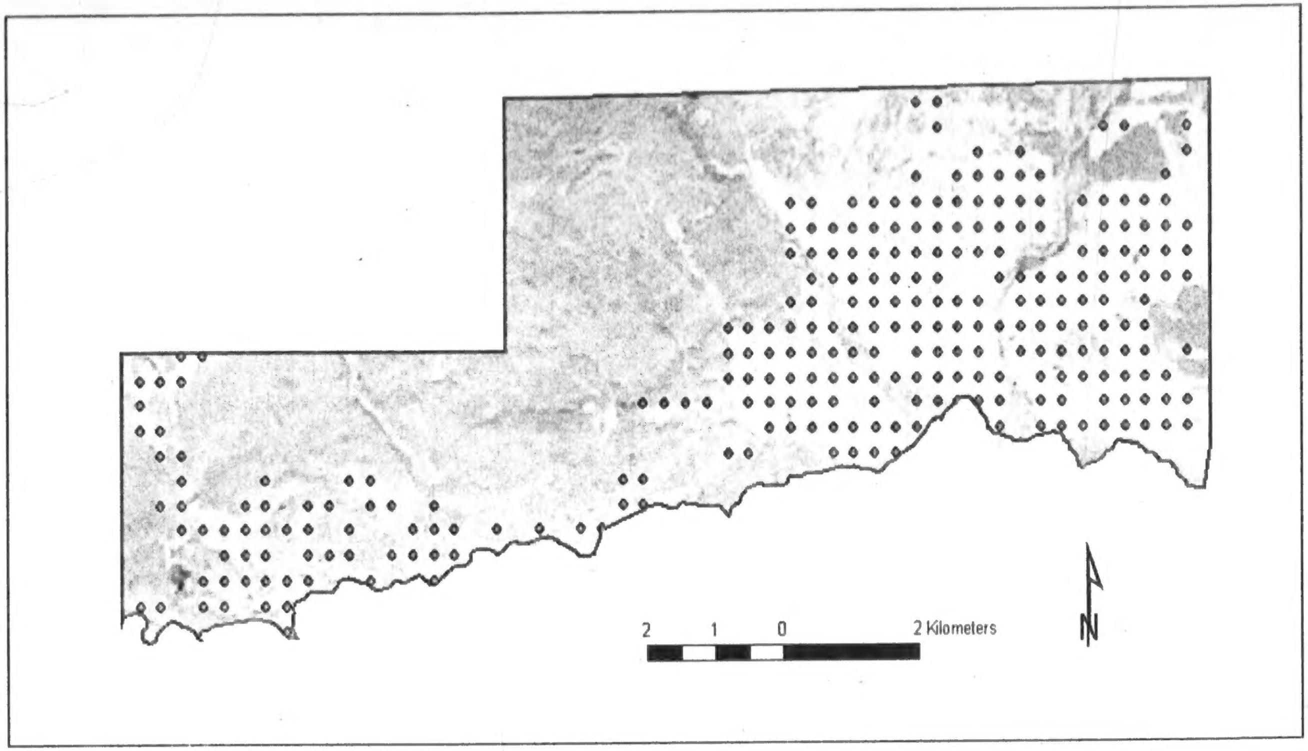
2
1
0
2 Kilometers
N

Fig. 2.1. Location of systematically placed sites where ungulate pellet groups were counted in winter and summer 2000-2002, Ya Ha Tinda Ranch.

of rough fescue within a 25-m^2 radius, topographic position (top of slope, midslope, midtoe, toe of slope, rolling, flat, low wet, seasonal wet, drainage, mini-drainages, floodplain, or wallow), elevation from a GPS, aspect (degrees), and visual estimates of distance (m) to cover, water (including the river, creeks, lakes, ponds, and seasonal drainages), and human activity (including campgrounds, roads, horseback riding trails, patrolled fencelines, and ranch buildings). Cover included any shrubs or trees that were estimated to be greater than 1.5 m tall and which could obscure approximately 75% of an adult elk. If water or human activity were not visible, an estimate was made based upon a TM satellite image from September 1998. The Site Severity Index (SSI), a second physiographic index that was expected to reflect local moisture and snow conditions, was calculated from the slope and aspect measurements following Nielsen and Haney (1998).

From digital GIS maps for each site I recorded vegetation class, soil type, and interpolated percent fescue. Vegetation class of the sample plot was determined from an existing map of 7 categories (closed conifer, open conifer, avalanche path, alpine, grassland, shrub, and rock/ice) created from Banff National Parks' Ecological Land Cover digital map (Holroyd and Van Tighem 1983, Holland and Coen 1983) and the Alberta Vegetation Inventory. Soil type was determined based upon a soil map that was produced by the Soil Survey Research Branch, Canada Department of Agriculture, prior to 1977 (McGillis 1977), and digitized for this research. A grid of percent basal cover fescue was interpolated from estimates taken in May 2001 at each site. The grid, versus direct measurements, was used in my analyses because rough fescue basal area was more easily estimated in spring after heavy winter grazing, and because the percent of fescue was not measured in the first summer survey. Observers were trained in visual estimation of variables and pellet group classification at the beginning of each seasonal survey to minimize observer error.

2.2.3 Data analyses

Spatial patterns and the variables related to elk distribution were investigated with [illegible] combination of geographical mapping and regression analyses. To describe the spatial pattern of elk use, I modeled the semivariance in the number of recent (black) elk pellets using a spherical model and a lag of 250 m for each season (Table 2.2). A 250-m lag was chosen because it was the minimum distance between surveyed plots. Mean standardized prediction errors between the observed and the modeled semivariance values ranged from 0.001 to 0.012 and standardized root mean square (RMS) values ranged from 0.953 to 1.006.

I used the model in ordinary kriging to interpolate broad-scale elk use patterns based on trend removal at 100% local scale (*Geostatistical analyst in ArcMap 8.1,* Environmental Systems Research Incorporated, California, USA). Percent rough fescue was interpolated in a similar manner from spring 2001 measurements. Standardized RMS values were used to evaluate model predictions.

Differences in the number of pellets counted between seasons were tested by pairing sites in time (e.g. counts from a the same site in spring 2001 and 2002 were compared) and using paired t-tests within SPSS 11.5 (SPSS Incorporated, Illinois, USA). To relate pellet counts to environmental factors, I used a generalized linear model (GLM) approach (Intercooled Stata 7.0, Stata Corporation, Texas, USA). Because count data are often lognormally distributed, and there were numerous sites where no pellets were observed in some seasons, I first determined the best model structure for the data by

Table 2.2. Parameters of the spherical model used in ordinary kriging to estimate the number of elk pellet groups at unsampled sites within grasslands at the Ya Ha Tinda Ranch in the Central East Slopes of Alberta.

Season	Nugget	Partial Sill	Range	Mean Standardized	RMS Standardized
Summer 2000	0.000037713	0.000021647	2220.3	0.0013	1.006
Winter 2001	0.000127120	0.000073649	1071.7	0.0084	0.9628
Summer 2001	0.000040338	0.000027981	1278.2	0.0025	0.9907
Winter 2002	0.000185530	0.000073397	1864.1	0.0122	0.9529

comparing logistic, Poisson, zero-inflated poisson, negative binonmial and zero inflated negative binomial regression models (Long 1997). I assessed model fit using the deviance-based dispersion of data (Hardin and Hilbe 2001), in addition to a Wald's Chi^2 test of the dispersion factor (α) for negative binomial regression, and a Vuong (1989) test of zero-inflation (Greene 1994). Once a model structure was chosen, I used a second-order Akaike's Information Criterion (AIC$_c$), (Burnham and Anderson 1998) to evaluate the best model from the candidate set of models for winter and summer seasons (Appendix I). Model selection allowed comparison of both model structure and model parameters (Burnham and Anderson 1998). I used a variance inflator (CLUSTER by site in Stata) to account for serial correlation associated with revisiting the same plots in different years (Rogers 1993, Williams 2000, Stata Corp. 2002).

Model predictions were evaluated with observed data using Pearson correlation for count models, and ROC curves to evaluate the goodness of fit of predictions from logistic models (Fielding and Bell 1997, Cumming 2000). Pseudo-r^2 values were calculated by dividing the difference in log likelihood (constant-only model minus the candidate model) by the log likelihood of the constant-only model. Model stability was assessed with a k-fold partitioning design (Fielding and Bell 1997) for cross validation because an independent data set was not available. Data were partitioned equally into 5 groups using Huberty's (1994) rule of thumb for model training, and the model was iteratively run on sets of 4 groups, with the remaining group reserved for validation (Boyce et al. 2002).

2.3 RESULTS

2.3.1 Effect of plot size on pellet counts

There were more zero counts on 25-m^2 than on 100-m^2 plots, particularly in the winter surveys. Using small plots resulted in counts approximately 15% higher than in large plots in winter and 50% in the summer (Fig. 2.2). However, pellet group counts in 25 m^2 were linearly correlated with counts at 100 m^2 ($P < 0.05$) (Figures 2.2A and 2.2B).

2.3.2 Temporal and spatial patterns in elk use

Elk pellet counts, adjusted to a per day basis (to account for different time intervals between sampling periods), were approximately 5 times higher during the winter than during the summer (Table 2.3). The summer elk pellet counts in 2001 tended to be lower than those of 2000, but the difference between years was not significant (Paired t-test, $P > 0.10$), whereas the winter elk pellet counts in 2002 were higher than those in 2001 (Paired t-test, $P < 0.005$).

In both years and seasons, elk used the eastern portion of the ranch to a greater extent than the western portion with higher use in 2002 (Fig. 2.3). Elk use shifted from the flats along the Red Deer River to the bench upslope along the Bighorn Creek from the growing season of 2000 to the growing season of 2001 (Fig. 2.4A). During the winters, elk pellet groups were highly concentrated around the Bighorn creek and this is consistent in 2001 and 2002 (Fig. 2.4B). In both years and seasons, elk pellet densities are high near areas of heavy human use, including the Bighorn campground and Bighorn falls.

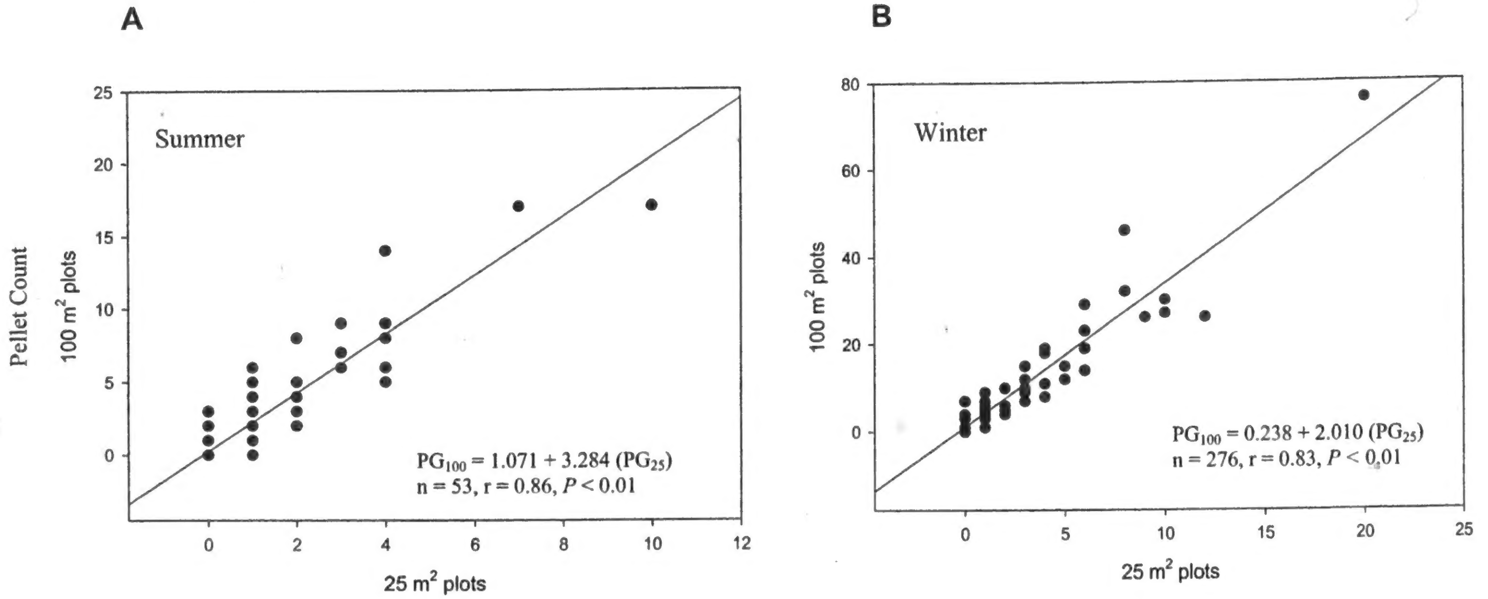

Fig. 2.2. Elk pellet groups counted in 25-m^2 and 100-m^3 plots in (A) summer 2001 and (B) winter 2001.

Table 2.3. Number of plots, minimum, maximum, mean, standard deviation, and coefficient of variation of the number of recent elk pellet groups (No./25 m^2) counted, and deposition rates (No./day) observed during winter and summer elk pellet surveys on the Ya Ha Tinda Ranch in Central Alberta.

Survey	N	Min	Max	Mean	SD	C.V. (%)	No./ day	SD	C.V. (%)
Summer 2000	263	0	8	0.57	1.07	188	0.004	0.008	200
Winter 2001	270	0	24	3.01	3.33	111	0.014	0.016	114
Summer 2001	276	0	10	0.42	1.04	248	0.003	0.007	233
Winter 2002	269	0	21	3.96	4.04	102	0.017	0.018	106

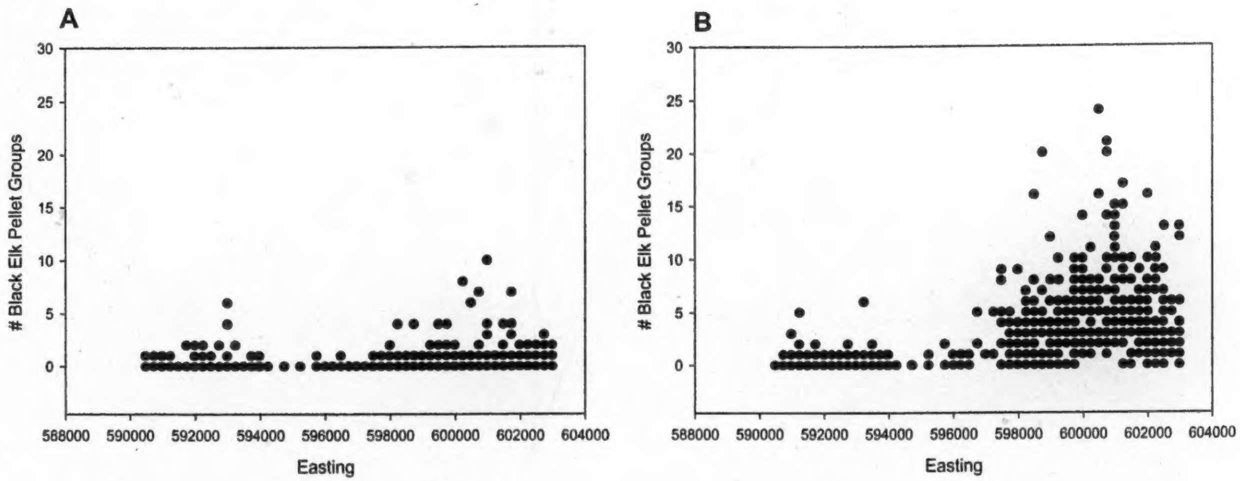

Fig. 2.3. East-to-west gradient of elk pellet groups counted on 25-m^2 plots during (A) summer and (B) winter surveys at the Ya Ha Tinda Ranch, September 2001 and May 2002.

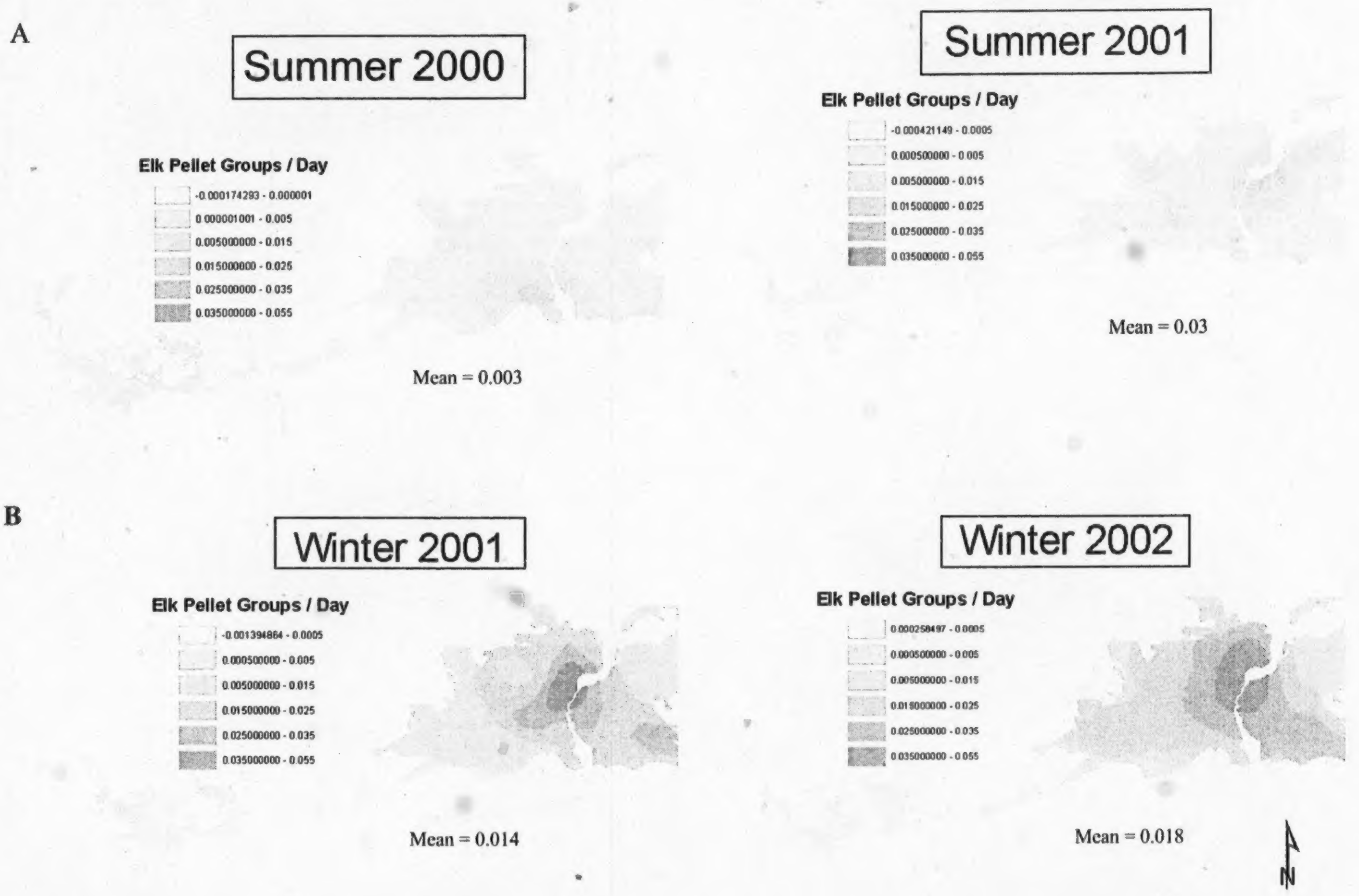
A
Summer 2000
Elk Pellet Groups / Day
-0.000174293 - 0.000001
0.000001001 - 0.005
0.005000000 - 0.015
0.015000000 - 0.025
0.025000000 - 0.035
0.035000000 - 0.055
Mean = 0.003
Summer 2001
Elk Pellet Groups / Day
-0.000421149 - 0.0005
0.000500000 - 0.005
0.005000000 - 0.015
0.015000000 - 0.025
0.025000000 - 0.035
0.035000000 - 0.055
Mean = 0.03
B
Winter 2001
Elk Pellet Groups / Day
-0.001394864 - 0.0005
0.000500000 - 0.005
0.005000000 - 0.015
0.015000000 - 0.025
0.025000000 - 0.035
0.035000000 - 0.055
Mean = 0.014
Winter 2002
Elk Pellet Groups / Day
0.000250497 - 0.0005
0.000500000 - 0.005
0.005000000 - 0.015
0.015000000 - 0.025
0.025000000 - 0.035
0.035000000 - 0.055
Mean = 0.018
N

Fig. 2.4. Extrapolation of elk pellet groups (no./$25m^2$/day) counted during seasonal surveys in the (A) summer 2000-2001 and (B) winter 2001-2002 at the Ya Ha Tinda Ranch, Alberta.

2.3.3. Factors Influencing Elk Distribution

Summer

Because the cover of standing plant material was higher on productive Chernozem soils in both years ($t = -3.21, -4.90$, $P = 0.002, 0.001$, $n = 276, 274$), I did not enter soil type and standing dead material into the same regression models. In contrast, because percent canopy cover of standing plant and percent basal cover of fescue were not strongly correlated ($r < 0.17$), and the correlation was significant in only one year (2000: $P = 0.004$, 2001: $P = 0.24$), I allowed these variables to enter the same models. I found no evidence ($r < 0.50$) for collinearity among the other environmental variables.

Summer elk pellet group counts were so low that pellet distribution was best modeled with logistic regression, reducing counts to presence or absence data (Table 2.4). From the candidate models examined (Appendix I), 5 top models were identified (Table 2.5). The most parsimonious model (for predicting elk distribution in summer) with a relatively high Δ AIC$_c$ (11.86) included the effects of standing plant cover, basal fescue cover, horse use, and year (Table 2.5). Based on the odds ratio, the probability of encountering elk pellets at a site in summer was 38% lower in 2001 than in 2002. The probability of encountering an elk pellet group in summer increased by 5% for every increase in percent fescue cover, increased by 3% with every increase in percent standing plant cover, and increased by 204% with each additional horse pellet group counted. The area under the ROC curve for this model was 0.70. On average, the model correctly predicted the presence of pellet groups 66 ± 1.32 % of the time based upon 5 validation models built from k-fold partitioning of the data.

Table 2.4. Coefficients of the candidate models for predicting elk distribution in summer and winter on the Ya Ha Tinda Ranch in Alberta, 2000-2001.

Parameter	Coefficient	SE_{robust}	Odds ratio or Incidence Rate Ratio	Z	*P*
SUMMER: $\Delta AIC_c = 11.86$, $AUC_{ROC} = 0.70\%$, Correct classification = 67%, Pseudo $r^2 = 0.09$, n = 550)					
%Fescue basal area	0.0479675	0.017592	1.049137	2.73	0.006
%Standing plant cover	0.0245406	0.004298	1.0284844	5.71	<0.001
Year	-0.481075	0.2044442	0.6181183	-2.35	0.019
# Horse pellet groups	0.712339	0.2897331	2.038754	2.46	0.014
Constant	-2.427338	0.3480839		-6.97	<0.001
WINTER: Alpha = 0.256 (0.0000), $\Delta AIC_c = 1.66$, Spearman rank r = 0.64, Pseudo $r^2 = 0.15$, n = 527)					
%Fescue basal area	0.0519882	0.0101740	1.053363	5.11	<0.001
Chernozem soil	0.3641839	0.0000244	1.439339	3.42	<0.001
Easting	0.0000864	0.1064128	1.000086	3.54	<0.001
Topslope	0.4495092	0.1429493	1.567543	3.14	<0.001
Year	0.2759010	0.0521384	1.317717	5.29	<0.001
Distance to tree cover (m)	0.0013373	0.0003081	1.001338	4.34	<0.001
Constant	-51.50328	14.674840		-3.51	<0.001
Inflation - Easting	-0.000518	0.0001024		-5.06	<0.001
Inflation - Constant	307.0847	60.553220		5.07	<0.001

Table 2.5. Top candidate models based on AICc for predicting summer and winter elk pellets in 2001and 2002 across the non-forested portions of the Ya Ha Tinda Ranch in Alberta, 2000-2001.

Structure	Parameters	Log likelihood	Wald Chi^2	df	*P*	AICc	ΔAICc
SUMMER							
Logistic	Year, %Fescue, SSI, %Standing material, Topslope, Distance to cover, # Dark horse pg	-307.85	63.90	8	<0.001	633.70	0
Logistic	Year, Grassland, SSI, %Standing material, Topslope, Distance to cover, #Dark horse pg	-310.896	57.86	8	<0.001	634.07	6.36
Logistic	Year, %Fescue, %Standing material, #Dark horse pg	-315.745	53.34	4	<0.001	639.56	11.86
Logistic	%Fescue, %Standing material, # Dark horse pg	-318.779	48.54	3	<0.001	643.60	15.90
Logistic	%Standing material, Year, # Dark horse pg	-319.308	51.37	3	<0.001	644.66	16.96
WINTER							
ZINB	Chernozem, Topslope, Year, Distance to cover *Inflation factors*: Easting, %Fescue	-1081.015	124.20	6	<0.0001	2178.31	0
ZINB	%Fescue, Chernozem, Topslope, Year, Distance to cover *Inflation factor*: Easting	-1082.74	142.25	6	<0.0001	2179.69	1.66
ZINB	Grassland, Chernozem, Topslope, Year *Inflation factor*: Easting	-1087.49	160.50	5	<0.0001	2189.19	11.16
Negative Binomial	%Fescue, SSI, Chernozem, Easting, Topslope, Year, Distance to cover	-1086.67	273.05	7	<0.001	2189.62	11.59
Negative Binomial	Grassland, Chernozem, Easting, Topslope, Year, Distance to cover	-1092.30	300.52	6	<0.001	2184.60	6.57

Winter

The percent standing material measured in the field was not an appropriate measure of forage availability in the winter surveys because of high off-take during the winter. Therefore I used chernozemic soils to reflect forage abundance. In an independent-samples t-test, sites described as having chernozemic soils had an average of 9.4% more standing material going into the winter than other soils on the ranch ($P <$ 0.001, n = 276).

Negative binomial and zero-inflated negative binomial model structures best fit the data of elk pellet group counts in winter. Of the eleven candidate models (Appendix I), 5 were identified as the best set of models (Table 2.4). The most parsimonious model with a relatively low Δ AIC$_c$ (1.66) was a zero-inflated negative binomial model using *easting* as an inflation factor (Table 2.5). Based on the incidence rate ratio (IRR), elk pellet groups increased by 32% in 2002 from 2001. The number of elk pellet groups increased by 5% for every increase in percent fescue cover, by 44% if the site was on chernozemic soils, by 57% if the site occurred at the top of a slope, by 13% for every kilometer away from hiding cover, and by 0.86% for each kilometer located further eastward. Based on the odds ratio for the zero-inflated component of the model, the probability of encountering elk pellets at a site decreased by 5% for each kilometer moved westward. Significant correlations ($P > 0.001$) between k-fold validation sets and observed counts were positive and ranged from 0.55 to 0.67.

2.4 DISCUSSION

2.4.1 Plot size

Counts of the number of pellet groups in 25-m^2 plots overestimated the count in 100-m^2 plots and this trend was greatest in summer when pellet counts were lowest. A larger edge-to-surface-area ratio in smaller plots may have resulted in a counting bias by increasing the probability of encountering a pellet group on the border of the plot (McKelvey et al. 2002). While > 50% of the pellet group was required to be within the plot border to be counted, the increase in decisions required for small plots likely exacerbated the observer error. However, pellet groups also are likely to be overlooked on large plots (Neff 1968). Because observer errors may occur at both plot sizes, I recommend remaining with a 25-m^2 plot size for long-term monitoring to increase sample efficiency and decrease errors between sampling periods due to missed groups when vegetation is taller and more dense.

2.4.2 Seasonal elk distribution

Declines in pellet group counts from winter to summer were consistent with migration from the ranch into the mountains between June and October (Hebblewhite 2002). A difference in the mean number of summer pellet groups in 2000 and 2001 was not detected in the pellet counts, and this was consistent with maximum ground counts of elk that were conducted by ranch staff. However, based on the summer distribution model there was a 38% decrease in the probability of detecting the presence of a pellet group across the ranch from 2000 to 2001. While the number of elk using the ranch may not have decreased in 2001, the spatial interpolation of elk pellet groups (Fig. 2.4) indicates elk use was more concentrated. In fact, pellet groups were present at 27% of sites in 2000 versus only 14% in 2001, indicating more concentrated use. In the summer of 2001, there were more areas with high pellet group deposition, but they were smaller and had shifted from the floodplains along the Red Deer River in 2000 to benches upslope and along the Bighorn creek in 2001 (Fig. 2.4A). This change in distribution may have been related to drier conditions in the growing season of 2001 than 2000. While precipitation data from the ranch is not available, the Alberta Environment weather station approximately 130 km northeast of the ranch in Red Deer, Alberta reported 507 mm (97.9% of long-term average) during the growing season of 2000 and only 327.3 mm (63.2% of long-term average) during the growing season of 2001 (Alberta Department of Agriculture 2002). I hypothesize that forage around the Bighorn creek retained more moisture, and that elk experienced greater thermal relief from shading from trees around the creek. The two patches of high use in the center of the grassland (Fig. 2.4) are within pastures where mares and young horses are provided supplemental hay and oats in spring. Elk may have been attracted to supplemental food, particularly in a drought year with lower forage production.

In contrast to summer counts, number of pellet groups counted on the ranch was higher in winter 2002 than in winter 2001, which was consistent with the winter modeling results. However, winter aerial counts of elk by provincial biologists do not support a population increase on the ranch from 2001 to 2002 (Alberta Sustainable Resource Development files, Rocky Mountain House). Because the spatial distribution of pellets across the ranch is similar between years, I suggest that elk used the grassland portion of the ranch more consistently throughout the winter of 2002, and that this was related to greater snow depths in 2002. Although snow depth data are not available for the ranch, I hypothesize that greater snow depths in the area during 2002 likely pushed elk onto the windswept grasslands for a greater proportion of the time in 2002.

In addition to the annual shifts in elk distribution, two patterns in the general spatial pattern of elk of the ranch were identified. First, it is evident from both Fig. 2.4 and from the winter distribution model that greater elk use occurs in the eastern portion of the ranch particularly in winter. Higher use on the eastern portion of the ranch may occur due to lower snow accumulation in the east or higher grassland productivity (Benn et al. 1988), which is supported by the increasing trend in standing plant cover from west to east ($r = 0.36$, $P < 0.001$) in fall prior to heavy winter grazing by elk. Alternatively, elk may concentrate on the eastern portion of the ranch to avoid predators. Current radio telemetry studies of wolf and elk movements on the ranch may provide more complete information on seasonal avoidance of predators.

The second spatial pattern is related to concentrated use around the Bighorn creek. All surveys, except summer 2000, documented high pellet counts at sites along the Bighorn creek. Elk likely congregate around the Bighorn creek because this location is a source of water, has a south-facing slope, and is surrounded by tree cover. In winter, south-facing slopes provide thermal benefits to the elk and increased forage availability due to more rapid snowmelt. The rapid snowmelt also affords south-facing slopes with a head start in spring green-up. Tree cover offers both shade and hiding cover, particularly in summer.

The spatio-temporal patterns of elk use on the Ya Ha Tinda Ranch are consistently associated with forage abundance because elk utilize areas with high percent of standing plant cover and with chernozemic soils. Although rough fescue cover is not correlated with standing plant cover, elk use also increases with fescue abundance, perhaps because rough fescue can be up to 68% ($\bar{x} = 24 \pm 17$ %) of May biomass and 58% ($\bar{x} = 20 \pm 13$ %) of August biomass (Chapter 3). Rough fescue is known to be important elk forage. For example, at Harrison flats, just south of the ranch, Morgantini and Russell (1983) reported *Festuca spp.* (most likely rough fescue) comprised 69.5% of elk winter diet based upon fecal fragment analysis, while on winter ranges in west-central Alberta, rough fescue has been reported to be 88.5% winter diet (Morgantini 1988). Recent fecal analysis from elk on the Ya Ha Tinda Ranch suggest that rough fescue comprises up to 49% during June green-up and an average 20% of the diet during winter (M. Hebblewhite, unpublished data, University of Alberta).

Nonetheless, elk distribution is influenced by factors other than forage abundance. For example, elk appear to concentrate during the winter in areas that are further away from cover and at the top of slopes. The inverse relationship with cover does not support an elk's need for cover in winter for mitigating thermal conditions. On winter ranges directly south of the ranch, Morgantini and Russell (1983) also suggested elk use of rough fescue communities was determined to a greater extent by forage abundance than by hiding cover, noting elk moved to a different portion of the meadow a majority of the time instead of running into forest cover when humans were working in the area.

Similar to Salter and Hudson's (1980) observation, elk were not excluded from ranch locations by horses in summer. The elk use, and the horses are pastured on, productive grasslands. In addition, elk may utilize areas near horses because salt licks are available or to avoid predation, as pastures are monitored by ranch staff. While horses do not exclude elk from using specific areas of the ranch seasonally, there may be short-term temporal segregation that could not be detected in this study.

While there was a positive relationship between elk and horses in the summer model, this relationship was not observed in the winter, when populations of both species increase (horses approximately 6-fold and elk approximately 4-fold). Horses are pastured at different locations during the summer and winter, and winter pasture locations tend to be in shrubby habitats with lower relative fescue cover. Horses are provided hay during the winter months, and elk have been observed eating the hay along with the horses; however, there was no seasonal relationship among elk pellet group counts and horse-feeding sites. I suggest this may be because elk spent shorter periods of time feeding at hay sites than they would at grazing locations, and as a result, seasonal pellet group counts do not detect this relationship.

In conclusion, elk use on the ranch, as indicated by pellet groups, is approximately 5 times higher in the winter than the summer. The percentage of elk not migrating, based upon pellet groups, is consistent with the concern that the proportion of elk staying on the ranch year-round is increasing. Elk use across the landscape is highly variable and differs in intensity and distribution among years, possibly related to precipitation patterns. As a result, the predictive capability of models developed across broad time scales is borderline between "low accuracy" and "useful application" for prediction (Swets 1988, Manel et al. 2001, Boyce et al. 2002). Nevertheless, it is clear that elk use areas with high forage availability and rough fescue in both seasons.

These patterns of elk grazing on the Ya Ha Tinda Ranch may contribute to changes in the composition and stability of the rough fescue grassland. For example, high urine and fecal deposition on the eastern portion of the ranch provides a readily available source of mineral N, which could assist in the recuperation of plants responding to defoliation during the growing season. Locations of the ranch with high levels of use in the summer (e.g. around Bighorn creek, the central pastures, and the floodplain along the river) should be monitored for changes in rough fescue abundance. Future research on patterns of seasonal grassland utilization of at the Ya Ha Tinda ranch should include fecal fragment analyses of horse and elk forage (or hay) selection (M. Hebblewhite, unpublished data, University of Alberta) as an indication of both selection and potential competition. In addition, investigation of the relationships between precipitation or predators on elk distribution could further explain pellet group patterns described in this study. Measures of forage offtake, quality and quantity within and surrounding the ranch should be also measured. Knowledge of available food resources, and whether they are currently utilized, would aid managers in decisions regarding the long-term management of Ya Ha Tinda elk herd and potential bison reintroduction.

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CHAPTER 3

EFFECTS OF SEASONAL DEFOLIATION ON A MONTANE FESCUE GRASSLAND: Productivity, diversity, and nutrient cycling

3.1. INTRODUCTION

Fescue grasslands are some of the most threatened communities in the Canadian Prairie Provinces (Vujnovic 1998). Concern about their loss due to development, woodland encroachment, exotic species and overgrazing has increased because only 5% of the grasslands remain in pre-settlement condition (Vujnovic 1998). The majority of fescue grasslands are in the foothills region east of the Canadian Rocky Mountains (Dormaar and Willms 1990), including the Parks Canada Ya Ha Tinda Ranch, in the Rocky Mountain foothills west of Sundre, Alberta. Today, the ranch is considered one of the most important winter ranges for elk (*Cervus elaphus*) in Alberta (Alberta Forestry 1986, Morgantini 1995). Increasing numbers of traditionally migratory elk using the Ya Ha Tinda during the growing season (Hebblewhite 2002) has caused concern for the long-term sustainability of the fescue grasslands on the ranch. For example, Morgantini (1988) reported only 25-50 (2-8% of wintering population) elk remained on the ranch during the summer in the early 1980s, whereas since 2000 between 150-200 (16-24%) elk were counted with a maximum count in summer 2002 of 350 (33%) (Hebblewhite 2002).

Most studies of grazing on mountain rough fescue (*Festuca campestris Rydb.*) communities have focused on the plant community responses to cattle grazing, and little is known of impacts from seasonal grazing by migratory, native herbivores. If rough fescue communities in the montane regions of central Alberta evolved primarily with winter grazing by native herbivores (Johnston and McDonald 1967), spring or year-round grazing may alter the organic C and mineral N dynamics within them, which may have implications for long-term sustainability, which depends upon the ability to conserve nutrients in the system. In general, large herbivores remove both litter and dead plant material reducing organic C input from plants (Coughenour 1991), but return fecal material of lower C:N ratio than plant inputs. In addition, studies indicate growing-season defoliation will increase relative allocation of C and N to plant shoots at the expense of plant roots (Holland and Detling 1990, Bardgett el al. 1998, Paterson and Sim 2000). Rough fescue allocated significantly less dry matter to roots when grazed by cattle during the growing season than when not grazed (King et al. 1998), and this contributed to lower root biomass on overgrazed sites (Johnston 1961, Dormaar and Willms 1998). Summer-grazed rough fescue grasslands also exhibited decreased total soil C and monosaccharides (Dormaar and Willms 1990, Dormaar et al. 1990, Dormaar and Willms 1998), which could decrease potential energy sources in the soil leading to declines in microbial activity (Dormaar and Willms 1998).

While grazing can result in decreased organic C input to the soil over the long-term, defoliation during the growing season also may cause a short-term flux in organic C, either by increases in root exudates (Holland et al. 1996, Hamilton and Frank 2001) or root turnover (Paterson and Sim 2000). The short-term C source after defoliation can stimulate microbial activity and N mineralization (Frank et al. 1994, Frank and Groffman 1998a, Tracy and Frank 1998, Frank et al. 2000). In Yellowstone National Park, Frank et al. (2000) suggested high levels of available N in the soil and N conservation were facilitated by rapid microbial turnover, likely a result of nematode predation on soil microorganisms, also known as the "microbial loop" (Bardgett et al 1998, Holland and Detling 1990, Merrill et al. 1994). Increased total soil N, NH_4-N and NO_3-N, combined with decreased microbial biomass, in summer-grazed rough fescue grasslands (Dormaar and Willms 1990, Dormaar et al. 1990, Dormaar and Willms 1998) could be the result of a microbial loop as described in other grazing systems.

As total soil mineral N increases under grazing, more N may become available to plants. Increased plant N concentrations have been hypothesized to exist as a result of reduced carbon allocation to roots, that limits microbial populations, and N mineralization creating positive N feedback from soil microorganisms (Holland and Detling, Holland et al. 1992, Bardget et al. 1998, Detling 1998, Frank and Groffman 1998b, Frank et al. 2000). However, grazing has also been reported to increase NO_3-N levels, particularly in later portions of the growing season (Holland and Detling 1990, Seagle et al. 1992, Frank and Groffman 1998a, Frank et al. 2000). Increased available soil N would suggest potential N-loss via leaching (Archer and Smeins 1991, Frank et al. 1994, Watson and Poland 1999), but studies in Yellowstone National Park (Frank et al. 1994, Frank et al. 2000) and simulation of grazing in the Serengeti (Seagle et al. 2000) did not find leaching to be a substantial source of N-loss. In both areas, plant and microbial N-uptake were indicated in the conservation of mineral N. With grazing, the NO_3-N:mineral N ratio increases in rough fescue grasslands (Dormaar et al. 1998), and this may be the result of decreased denitrification/net N mineralization ratio or to autotrophic nitrifiers, which use NH_4-N as an energy source instead of carbon (Kaye and Hart 1997) . Combined with reduced leaching, reported by Frank et al. (2000), under all but extreme levels of grazing, a lower proportion of denitrification and/or increased nitrification may account for increased levels of NO_3-N in grazed soils.

I conducted a 2-year clipping experiment, within and outside 6 exclosures in the rough fescue grasslands at the Ya Ha Tinda Ranch, and subjected vegetation at the plot and individual fescue plant level to seasonal clipping treatments that represented the expected changes in grazing regimes if elk become non-migratory. My objectives were to (1) document initial, short-term changes in community composition; (2) compare differences in above- and below-ground biomass as a result of seasonal defoliation regime; (3) relate nitrogen pools and leaching to seasonal defoliation; and (4) identify demographic and morphologic fescue response to seasonal defoliation regimes.

I hypothesized that changes in community composition would be minimal after two years, but aboveground biomass (living and dead) and belowground biomass (living plus dead) of rough fescue would decrease with frequency of clipping. I expected root biomass and volume in plants clipped during winter would not differ during the growing season from nondefoliated plants, while winter/spring clipping would result in temporary root losses exhibited in June that were not evident by the end of the growing season. I expected aboveground production would be lower under summer clipping than all other defoliation treatments, and this reduction would be associated with the lowest root biomass and volume. I hypothesized that a shift from winter clipping to clipping in the growing season would increase soil N mineralization, relative net nitrification and plant N concentrations, but total plant N available to aboveground herbivores at the end of the growing season would be lower with continued defoliation during the summer because of reduced plant growth. I expected leaching would not be different among clipping treatments.

3.2 METHODS

3.2.1 Study sites

The Ya Ha Tinda Ranch is an area of approximately 440 ha located approximately 5 km east of the Banff National Park boundary along the Red Deer River Valley in Alberta at 51° 45' latitude and 115° 35' longitude. Average elevation of Ya Ha Tinda is about 1550 m. The climate is Cordilleran with westerly winds that, in addition to low precipitation, keep the grasslands mostly snow-free in the winter (Benn et al. 1988). Geologic parent material consists of glacial till (Seel and Wiebe 1988) and colluvial veneers (AGRA Earth and Environmental 1998). Grassland soils consist primarily of Orthic Black and Eluviated Black Chernozems, Orthic Melanic Brunisols, Orthic Regosols, and Orthic Grey Luvisols (McGillis 1977, AGRA Earth and Environmental 1998). Vegetation of the Ya Ha Tinda Ranch consists of nearly 30% grassland that has been described as a variant of the *Festuco-Stipetum richardsoni* association (Looman 1969). Common grasses include rough fescue, rocky mountain fescue (*F. saximontana*), June grass (*Koeleria macrantha*), Hooker's oat grass (*Helicotrichon hookeri*), slender wheat grass (*Agropyron trachycaulum*), hairy wild rye (*Elymus innovatus*), fringed brome (*Bromus ciliatus*), and smooth brome (*Bromus inermis pumpellianus*) (AGRA Earth and Environmental 1998). Forests consist primarily of lodgepole pine (*Pinus contorta*), trembling aspen (*Populus tremuloides*), and white spruce (*Picea glauca*), while common shrubs include bog birch (*Betula glandulosa*), shrubby cinquefoil (*Potentilla fruticosa*) and willow (*Salix* spp.) (McGillis 1977).

3.2.2 Field experiments

Six exclosures were placed across the ranch with equal numbers in 2 productivity and 3 elk use levels. Productivity of the site was based upon primary and secondary forage range, defined by soil maps and productivity data reported by Seel and Wiebe (1988) and AGRA Earth and Environmental Ltd. (1998). Grazing levels at each exclosure initially were based on park staff knowledge. Post-stratification of exclosure sites based on pellet group counts (Chapter 2) verified and quantified the initial grazing levels as: high winter (4.90 ± 4.35 pellets/day, mean ± SD) and low summer (0.91 ± 0.44) (HL) use, high winter (8.48 ± 2.29) and high summer (1.12 ± 0.47) (HH) use, or sites in which elk use was high in winter (11.15 ± 1.08) and summer (1.33 ± 0.45), but no horse use (E).

Clipping treatments

Seasonal defoliation treatments were designed to compare grazing levels that might occur when elk are migratory, leaving after winter or spring, and if elk use becomes less migratory. At each of the 6 exclosures, three 2-m^2 plots were subjected to each of the clipping treatments (no clipping, winter clipping, winter and spring clipping, or year-round clipping) and natural grazing treatment (elk and horse grazing outside the exclosure). A buffer of at least 50 cm was placed between plots. Clipping heights (4 cm in winter, 3 cm in spring, and 4 cm in summer) were determined based upon average height of defoliation outside exclosures visually estimated across sites. Plots were clipped during the dormant season between 27 January - 15 April, during spring between 12-19 May, and during summer between 21-24 June in 2001 and 2002. Measurements within plots taken in 2002 were used to reflect the short-term responses to these clipping treatments.

Species composition and aboveground biomass

Species composition and aboveground biomass were sampled between 29 May - 10 June and 1-17 August 2002 within 0.25 m^2 ($n = 90$) in the center of the plot by the point-intercept method, using a 50-cm pin frame with 10 needles inclined at 45° (Wilson 1960, Floyd and Anderson 1987). The point-intercept method was selected in order to simultaneously measure biomass and composition across multiple vegetative layers. The pin frame was placed at 5-cm increments within plots and all foliage intersected on the path to the ground was recorded, by plant group in spring and by species in summer, resulting in 100 readings per plot. Vegetation hits were recorded as aerial or basal (i.e. the point in which the plant originates from the soil) and non-vegetative ground cover measurements (e.g. bare ground) were calculated based only upon basal hits. A double sampling approach was used to estimate aboveground biomass by estimating the relationship between pin counts and vegetative biomass from additional plots ($n = 107$) outside the exclosures. Plant material was clipped and oven-dried for 48 hours at 50° C. I used the following relationship developed between pin counts and clipped biomass collected in both 2001 and 2002 to predict aboveground biomass ($r^2 = 0.85$):

$$\ln(\text{biomass}) = 1.759 + 0.007\,(\text{pin count}) + 0.585\,(\text{August}) - 0.348\,(\text{year2002}).$$

Total production was calculated as the sum of plant biomass estimated in August plus previously clipped biomass. Percent composition was calculated as the number of hits for each plant group, litter, and bare ground divided by the total number of hits.

Shannon-Wiener diversity (H) and evenness (E) were calculated based upon the number of hits for each species and excluded litter and bareground.

Belowground biomass

Two root cores (5 cm diameter x 15 cm depth) were taken randomly from within the remaining 1.75-m^2 area of the plot, excluding a 10-cm buffer around the species composition sub-plot and the 2-m^2 plot edge, in each replicate plot ($n = 180$) in summer (9-18 June) and early fall (18-25 September) in 2002. Aboveground plant material from root cores was cut at 2 cm prior to coring, oven-dried for 48 hours at 50°C, and weighed. Root cores were placed in coolers in the field (< 10 hours), refrigerated at 4°C in the lab, and processed within 3 months. Due to rocky soils, all root and soil cores were divided into 0-5 cm and 5-15 cm depths. Any random samples that were below a minimum depth of 5 cm were disregarded and an additional random sample was taken from the plot. Roots (0-5 cm depth, 0.000076 m^3) were washed, collected in 4-mm mesh sieves, separated from belowground crowns, and scanned for root length at the 4-mm mesh size. After scanning, roots were separated into herbaceous or woody roots (if > 2mm diameter), oven-dried for 48 hours at 50°C, and weighed. Roots were washed in a Delta-T Root Washer (Delta-T Devices, Ltd.), scanned at 300 dpi, with a 2-mm^2 filter, on an Epson Expression 800 scanner, and analyzed for length using the REGENT's method in WinRHIZO (Regent Instruments, Inc.).

Soil and plant nitrogen

Two soil samples (5 cm diameter x 15 cm depth) were collected from each plot in 12-19 May and 21-27 August 2002, frozen (-18ºC), and analyzed for mineral N and soil moisture ($n = 180$). At the same time, mineralization rates were measured *in-situ* using soils incubated for 28 days in 2 PVC cores (5 cm diameter x 15 cm depth) with ion-exchange resin bags placed at the bottom to collect leaching N as described by Raison et al. (1987) and modified by Hart and Firestone (1989). This *in-situ* method is quantitative and less destructive than methods such as the buried-bag technique (Raison et al. 1987). The use of cores minimizes competition with roots, as experienced by ion-exchange resin bags alone (Binkley 1984) and prevents accumulation of N, a problem experienced with polyethylene bags (Hart and Firestone 1989). *In situ* net N mineralization was calculated as the difference between pre- and post-incubation mineral N. Average site bulk density was measured by arbitrarily sampling 6 cores within a paired, unfenced area next to each exclosure. Bulk density was determined by dividing oven-dried (100°C) soil mass by core volume at each depth. Roots and rocks > 1 cm were removed from field-moist soil by hand, just prior to sub-sampling for laboratory analysis of mineral N, and soil moisture was determined gravimetrically. A sub-sample of soil from each core was analyzed for mineral N (NO_3-N, NH_4-N) by shaking 10 g (oven-dry equivalent) of field moist soil with 50 mL of 2 mol/L KCl for 30 min and filtering through VWR brand 410 filter paper (Maynard and Kalre 1993). Extractant was frozen in vials (-18°C) and analyzed with a Technicon Autoanalyzer II (Industrial Methods #90-70 and #100-70W-B, Technicon Industrial Systems, October 1973) by the Renewable Resources High Volume Lab at the University of Alberta.

Aboveground plant material was collected from *in situ* mineralization tubes during June and September 2002. Shoots were oven dried at 50°C for 48 hours, sorted into live (green) and dead (brown) material, and weighed. Green material was ground to a fine powder in a ball grinder and analyzed for CN content with a Carlo-Erba

Autoanalyzer NA1500 by the Renewable Resources Stable Isotope Lab at the University of Alberta. Green shoot material was analyzed for CN as an indicator of living plant material able to consume available soil N during the 28-day mineralization trial. This assumed that shoot death and senescence over the course of the trials were limited.

Individual fescue plants

Inside the exclosures at each site, 25 fescue plants were marked with a small, plastic coated wire wrapped around the base and subjected to the same 5 defoliation treatments as described above. Average plant height was measured from the ground to the average height of living tillers. Tiller height and reproductive status was measured for 3 arbitrarily selected tillers. Reproductive status was recorded as vegetative or floral based on the presence of seedheads. Basal area was calculated according to protocol described by the United States Forest Service (Cook et al. 1992), wherein plant shape, defined as circular, elongated, arced, and ringed, was considered in the determination of area. Because the program software and algorithms were no longer available through the Forest Service, basal area calculations were developed for this study (Appendix I). Plant measurements were taken before each clipping treatment. Individual rough fescue plants were harvested 21-24 August 2002 after 2 years of clipping treatments. Shoots were dried, weighed, and analyzed for CN as previously described, except C and N were measured for total shoots for which I composited alive and dead material. Root cores (5 cm x 15 cm) were taken from the center of each plant, placed in coolers in the field, and frozen until analyses. Roots (0-5 cm depth) were washed with a Delta-T Root Washer and analyzed for root biomass and length in the same method as root cores from plots.

Statistical analyses

Pearson correlations were used to test relationships between soil and plant variables within plots across sites. Differences in plant and soil values from plots among clipping treatments and sampling dates within each year were analyzed using a GLM procedure with repeated measures in SPSS 11.5 (SPSS Incorporated, Illinois, USA), using a significance value of $\alpha = 0.10$. A less conservative α-value was selected to allow detection of potential initial differences under the highly variable soils factors and the short-term nature of the experiment. The estimated mean squares were calculated using the Type III sums of squares error term. Least Squares Difference (LSD) post-hoc tests were used to determine treatment differences within seasons. Sub-samples within treatments at each exclosure were averaged and statistical results are means of 6 replicates. Differences among plant morphology and nutrient status within individual fescue plants among clipping treatments and sampling dates were also analyzed with repeated measures in the manner described above. Sub-samples within treatments (n = 2-5, as a result of lost or dead plants) at each exclosure were averaged and statistical results for individual plants were means of 6 replicates.

3.3 RESULTS

3.3.1 Ungulate use

Although elk use at exclosures was consistently higher in winter (8.18 ± 3.89, $\bar{x} \pm$ SD, pellet groups ha^{-1} day^{-1}) than in summer (1.12 ± 0.42 ha^{-1} day^{-1}), relative use at the individual exclosures (Table 3.1) was not correlated between seasons (Spearman rank correlation: $r_s = 0.40$, $P = 0.43$ n = 6). Only at the West Lakes exclosure was elk use consistently low in winter and summer. Average growing season offtake on grazed

Table 3.1. Relative elk use and percent aboveground plant biomass removed (offtake) by clipping and by elk at the 6 exclosure sites where clipping experiments occurred during the growing season. Relative elk use is indicated by interpolated elk pellet counts (see Chapter 2). Grazing offtake: annual production on control plots inside exclosure minus annual production on naturally grazed plots/ annual production on control plots x 100. Clipping offtake: total biomass cut in winter, spring or spring and summer / annual production on clipped plot x 100.

	Pasture	Bog Birch	East Slope	Elk Hill	Scalp Creek	West Lakes	$\bar{x} \pm$ **SD**
Relative elk use							
Winter elk pellet groups ha^{-1} day^{-1}	10.74	8.51	11.17	11.14	6.21	1.30	8.2 ± 3.9
Summer elk pellet groups ha^{-1} day^{-1}	0.72	1.25	1.62	1.05	1.52	0.57	1.1 ± 0.4
Grazed offtake (%)							
Winter	94	85	98	97	97	95	94.3 ± 4.8
Growing season	26	94	72	74	63	65	65.7 ± 22.3
Clipped offtake (%)							
Winter	72	91	81	69	65	67	74.2 ± 10.0
Spring	23	11	8	10	18	13	13.8 ± 5.6
Year-round	86	46	51	67	70	57	62.8 ± 14.6

plots was 65.7 ± 22.5% in the growing season and 94.3 ± 4.3% in winter (Table 3.1). Growing season estimates should be considered a minimum because they do not include regrowth. Clipping to simulate grazing resulted in removal of total production averaging 74.2 ± 10.0 in winter, 13.8 ± 5.6 in spring, and 62.8 ± 14.6% on year-round plots (Table 3.1).

3.3.2. Species composition and aboveground biomass

Species richness did not differ in plots among clipping regimes in August 2002, but both species diversity (Shannon-Wiener index of diversity *H*) and evenness (Shannon-Wiener index of evenness *E*) decreased with clipping frequency (Table 3.2). Of all treatments, unclipped plots (C) had the greatest diversity ($P = 0.03$). Winter (W) and Winter-Spring (WS) clipping treatments also had greater diversity than Year-round (YR) clipped plots. Naturally grazed (G) sites outside the exclosures had diversity levels intermediate to WS and YR treatments. Evenness was greater on C, W, and WS plots than YR and G plots.

Differences in percent composition of plant groups were also evident by the second year of clipping treatments (Table 3.3). Defoliation decreased the percent composition of grass species including rough fescue, but fescue, in contrast to grasses generally, remained low at the end of the growing season when clipping was continued into the summer. The ratio of dead to live grasses was 2 to 3 times higher on unclipped plots in spring and summer than on all other plots ($P < 0.001$), but there were no significant differences among clipped and grazed plots. At the end of the growing season, the percent composition of sedges was generally higher in plots continually clipped during the growing season than clipped only in winter or spring (Table 3.3). In

Table 3.2. Plant species richness, Shannon-Weiner diversity, and evenness in fescue grasslands after 2 years of seasonal clipping treatments and natural grazing at the Ya Ha Tinda Ranch in southwestern Alberta, July-August 2002.

		Control (C)	Winter (W)	Winter Spring (WS)	Year-round (YR)	Grazed (G)	P
# Species	$\bar{x}$	20.61	18.61	20.56	19.17	19.22	0.825
	SD	4.12	2.99	4.01	3.62	3.13	
Diversity	$\bar{x}$	2.45^{c}	2.08^{bc}	2.10^{bc}	1.52^{a}	1.59^{ab}	0.030
	SD	0.36	0.41	0.40	0.60	0.79	
Evenness	$\bar{x}$	0.82^{b}	0.71^{b}	0.70^{b}	0.51^{a}	0.53^{a}	0.009
	SD	0.07	0.11	0.09	0.17	0.25	

a-c Means followed by different letters differ significantly ($P \leq 0.10$)

Table. 3.3. Aboveground biomass (g/m^2), percent vegetative composition, and percent bare ground in fescue grasslands after 2 years of seasonal clipping treatments and natural grazing at the Ya Ha Tinda Ranch in southwestern Alberta, June and September 2002.

		June					September					P		
		Control	Winter	Winter Spring	Year-round	Grazed	Control	Winter	Winter Spring	Year-round	Grazed	Season	Treat-ment	SxT
Annual production *	$\bar{x}$						932.50	257.53	176.56	129.71			0.268	
	SD						1588.66	206.35	79.91	63.24				
Total biomass	$\bar{x}$	496.31^{b}	56.22^{a}	37.26^{a}	39.48^{a}	40.79^{a}	1270.84^{b}	247.82^{a}	153.43^{a}	79.25^{a}	128.26^{a}	0.061	0.087	0.332
	SD	576.92	11.10	3.81	2.93	28.41	2000.44	192.73	67.15	47.51	99.03			
Green biomass	$\bar{x}$	157.97^{b}	40.49^{a}	29.07^{a}	29.89^{a}	29.75^{a}	610.86^{b}	181.10^{ab}	121.62^{a}	60.96^{a}	97.45^{a}	0.037	0.004	0.361
	SD	137.56	9.55	3.27	4.73	12.01	956.93	171.98	59.27	48.71	69.74			
Green:Dead biomass	$\bar{x}$	0.89^{a}	2.77^{ab}	4.35^{b}	3.54^{b}	6.76^{c}	0.88^{a}	2.92^{ab}	3.89^{b}	3.60^{b}	3.91^{b}	0.245	0.004	0.349
	SD	0.51	0.85	2.39	1.56	4.46	0.25	2.83	1.54	3.38	1.44			
All grasses (%)	$\bar{x}$	55.36^{c}	41.42^{b}	29.50^{a}	31.61^{a}	28.90^{a}	58.65^{c}	49.54^{b}	44.78^{b}	30.56^{a}	42.58^{b}	<0.001	<0.001	<0.001
	SD	7.42	3.99	8.65	5.08	8.12	7.33	6.41	7.76	8.38	7.20			
Non-fescue grass (%)	$\bar{x}$	30.62^{b}	19.57^{a}	14.69^{a}	16.61^{a}	16.83^{a}	29.09	24.34	21.31	17.34	21.32	0.002	0.054	0.053
	SD	10.19	8.86	3.27	9.02	7.78	10.77	8.50	9.18	8.66	6.76			
Fescue (%)	$\bar{x}$	24.75^{c}	21.85^{bc}	14.81^{a}	15.27^{ab}	12.07^{a}	29.57^{c}	25.20^{bc}	23.47^{bc}	13.22^{a}	21.26^{b}	<0.001	0.037	<0.001
	SD	7.80	9.49	8.10	3.80	4.58	9.34	7.07	10.35	3.58	7.76			
Carex (%)	$\bar{x}$	11.56	13.36	13.99	15.63	13.11	8.87^{a}	10.40^{a}	12.03^{ab}	14.78^{b}	10.02^{a}	<0.001	0.118	0.625
	SD	4.05	3.28	2.91	3.39	3.18	2.62	3.38	4.43	4.70	2.10			
Forb (%)	$\bar{x}$	12.46	11.64	14.61	13.39	9.37	9.64	9.21	10.40	10.41	7.89	<0.001	0.615	0.676
	SD	6.06	4.53	6.04	5.94	3.58	5.30	4.78	3.63	4.42	2.81			
Shrub (%)	$\bar{x}$	0.01	0.15	0.16	0.32	0.61	0.07^{a}	0.15^{a}	0.17^{a}	0.28^{a}	0.68^{b}	0.647	0.139	0.950
	SD	0.02	0.32	0.29	0.40	0.87	0.09	0.25	0.32	0.35	0.68			
Litter (%)	$\bar{x}$	15.97^{a}	26.51^{b}	33.32^{c}	32.28^{c}	37.32^{c}	15.18^{a}	20.95^{ab}	23.16^{bc}	32.97^{d}	27.75^{cd}	<0.001	<0.001	0.003
	SD	4.14	2.33	2.96	1.69	10.16	4.94	5.10	5.09	6.59	10.57			
Bare ground (%)	$\bar{x}$	0.05^{a}	0.22^{a}	0.18^{a}	0.13^{a}	1.28^{b}	0.00^{a}	0.00^{a}	0.00^{a}	0.00^{a}	0.02^{b}	0.004	0.016	0.016
	SD	0.09	0.27	0.27	0.25	1.37	0.00	0.00	0.00	0.00	0.02			

* Production includes clipped biomass

a-c Within a season and variable, means followed by different letters differ significantly ($P < 0.10$)

contrast to graminoids, there was no difference in percent composition of forbs (*P* = 0.615) as a result of defoliation treatments. The percent composition of shrubs was 2 to 9 times greater on grazed than clipped or unclipped plots (*P* = 0.09). Defoliation increased the percent of bare ground (*P* = 0.016) and litter (*P* < 0.001). The percentage of hits that were bare ground differed significantly among treatments in both seasons; however, this was primarily due to a 5.8 - to 25.6 -fold increase in bare ground during spring and an approximately 5-fold increase in summer on grazed plots as compared to clipped or unclipped plots.

At 5 of the 6 exclosures, standing biomass at the end of the growing season averaged 191.3 ± 262.4 g m^{-2}, which was 205% higher than in spring. One exclosure (Bog Birch) was much more productive, with standing biomass averaging 1299.1 ± 2214.0 g m^{-2}. Even with the exclusion of the most productive exclosure, there were no significant differences in annual production among clipping treatments; however, standing biomass at the end of the growing season tended to decrease with frequency of clipping (Table 3.3).

Unclipped plots had greater standing biomass than clipped or grazed plots in both spring and summer (*P* = 0.087, Table 3.3); however, this was primarily due to the removal of standing dead biomass with defoliation. The ratio of green to dead standing biomass on unclipped plots was at least 3 times lower than on WS, YR, and G plots in both seasons (*P* = 0.004). In spring, grazed plots also had a greater proportion of green standing biomass than all other treatments. In both seasons there was a decreasing trend in biomass as the frequency of clipping increased (Table 3.3).

3.3.3. Root biomass and morphology

Root biomass (g/core) and length (mm/core) were correlated, with stronger correlations between herbaceous root biomass and root length (June: $r = 0.82$, $P < 0.001$; September: $r = 0.78$, $P < 0.001$) than total root biomass and length (June: $r = 0.45$, $P = 0.012$; September: $r = 0.33$, $P = 0.077$). Root biomass, average diameter, and volume exhibited significant increases from June to September, while root length was more variable (Table 3.4). Root growth (biomass and length) was associated with higher soil moisture in both June ($r > 0.61$, $P < 0.001$) and September ($r > 0.36$, $P < 0.05$).

There were no significant differences in root biomass (total, woody or herbaceous), root length or average root diameter in either June or September as a result of two-year clipping treatments (Table 3.4), but the trend was that both herbaceous root biomass and total root length was lowest on grazed sites outside the exclosure in both June and September. Root:shoot ratios differed among treatments and seasons and were highest at naturally grazed sites in both time periods (Table 3.4).

3.3.4 Nitrogen pools

Mean concentrations of mineral N in the top 5 cm of soil ranged from 2 to 6 times those of mean concentrations at the 5-15 cm depth. Because soils were too rocky to consistently sample the 15-cm depth (mean core depth = 11.6 cm ± 3.02), mineral N pools were reported generally only for the 5-cm depth. However, soil NO_3-N was positively correlated at the 0 to 5-cm and 5 to 15-cm depths in both sampling periods ($P < 0.01$, $r = 0.60 - 0.74$, $n = 90$) and soil NH_4-N was correlated at the two depths in June ($P < 0.05$, $r = 0.43$, $n = 90$), but not in September.

Table 3.4. Root biomass (g/core) in fescue grasslands after 2 years of seasonal clipping treatments and natural grazing at the Ya Ha Tinda Ranch in southwestern Alberta, June and September 2002.

		June					September					*P*		
		Control	Winter	Winter Spring	Year-round	Grazed	Control	Winter	Winter Spring	Year-round	Grazed	S	T	SxT
Herbaceous root biomass (g/core)	$\bar{x}$	0.350	0.393	0.330	0.370	0.318	0.734	0.601	0.686	0.592	0.528	<0.001	0.229	0.140
	SD	0.107	0.074	0.077	0.054	0.026	0.221	0.117	0.079	0.163	0.115			
Woody root biomass (g/core)	$\bar{x}$	0.318	0.243	0.208	0.215	0.464	0.276	0.293	0.307	0.226	0.371	0.928	0.444	0.818
	SD	0.085	0.112	0.105	0.143	0.683	0.097	0.117	0.109	0.109	0.090			
Root:shoot ratio	$\bar{x}$	3.019 ^{ab}	3.090 ^{ab}	4.237 ^{b}	2.725 ^{a}	4.653 ^{b}	5.242 ^{a}	3.425 ^{a}	4.348 ^{a}	4.990 ^{a}	8.522 ^{b}	<0.001	0.006	0.042
	SD	1.165	1.528	1.671	1.399	1.428	1.894	0.812	0.893	2.087	4.709			
Root length (mm/core)	$\bar{x}$	1671.02	1817.13	1579.52	1573.31	1543.07	1791.65	1758.12	1963.17	1564.99	1547.76	0.089	0.238	0.065
	SD	354.00	325.86	218.35	159.91	242.87	354.03	80.79	217.70	334.50	261.36			
Avg. root diameter (mm)	$\bar{x}$	0.372	0.372	0.375	0.363	0.389	0.490	0.464	0.443	0.459	0.450	<0.001	0.564	0.055
	SD	0.020	0.023	0.017	0.027	0.0[illegible]1	0.015	0.036	0.030	0.035	0.054			
Root volume (cm^3/core)	$\bar{x}$	1.882	1.966	1.763	1.658	1.814	3.487	3.041	3.025	2.704	2.525	<0.001	0.390	0.161
	SD	0.646	0.418	0.340	0.392	0.338	0.851	0.580	0.380	0.794	0.877			

a-b Within a season and variable, means followed by different letters differ significantly ($P \leq 0.10$)

Table 3.5. Average plant and soil nitrogen pools (0-5 cm) taken from PCV cores at 6 exclosure sites after 2 years of seasonal clipping treatments and natural grazing at the Ya Ha Tinda Ranch in southwestern Alberta, June and September 2002.

		Pasture	Bog Birch	East Slope	Elk Hill	Scalp Creek	West Lakes	*P*
June								
Soil moisture (%)	$\bar{x}$	50.9^{c}	56.3d	49.7bc	46.3^{b}	43.1^{ab}	36.2a	<0.001
	SD	1.43	3.69	1.23	4.26	2.63	2.50	
Shoot biomass (g)	$\bar{x}$	0.089	0.081	0.144	0.136	0.118	0.081	0.260
	SD	0.085	0.258	0.099	0.338	0.034	0.034	
Root biomass (g)	$\bar{x}$	0.650^{b}	0.738^{b}	0.712^{b}	0.704^{b}	0.485^{a}	0.477^{a}	0.005
	SD	0.085	0.082	0.103	0.215	0.071	0.117	
June NO_3-N $\mu g\ g^{-1}$ soil	$\bar{x}$	78^{c}	32^{a}	68^{bc}	48^{ab}	54^{ab}	59^{b}	0.011
	SD	16.32	23.21	14.21	15.64	5.34	27.62	
June NH_4-N $\mu g\ g^{-1}$ soil	$\bar{x}$	34^{a}	145^{c}	65^{b}	25^{a}	30^{a}	16^{a}	<0.001
	SD	11.24	30.79	11.66	5.21	6.23	6.21	
Net mineralization mg N kg^{-1} day^{-1}	$\bar{x}$	1^{abc}	5^{d}	2^{bc}	1^{ab}	1^{abc}	1^{abc}	<0.001
	SD	0.74	1.84	0.44	0.65	0.64	1.20	
Net Nitrification mg N kg^{-1} day^{-1}	$\bar{x}$	1	1	1	0	1	1	0.400
	SD	0.50	0,74	0.52	0.62	0.20	1.08	
NO_3-N leached $\mu g\ g^{-1}$ resin	$\bar{x}$	6^{b}	2^{a}	8^{bc}	5^{ab}	8^{bc}	11^{c}	0.008
	SD	3.43	0.50	3.81	1.35	4.04	4.52	
September								
Soil moisture (%)	$\bar{x}$	37.1^{a}	51.5^{d}	37.8^{abc}	31.7^{ab}	40.9c	35.6^{a}	<0.001
	SD	1.06	4.31	1.55	2.11	2.87	2.40	
Shoot biomass (g)	$\bar{x}$	0.355	0.873	0.614	0.424	0.546	0.592	0.090
	SD	0.127	0.215	0.522	0.137	0.148	0.270	
Root biomass (g)	$\bar{x}$	0.333^{a}	0.436^{b}	0.314^{a}	0.380^{ab}	0.339^{a}	0.311^{a}	0.040
	SD	0.089	0.077	0.043	0.061	0.051	0.045	
NO_3-N $\mu g\ g^{-1}$ soil	$\bar{x}$	20^{b}	4^{a}	19^{b}	18^{b}	21^{b}	18^{b}	<0.001
	SD	4.29	2.02	5.01	2.23	0.28	2.08	
NH_4-N $\mu g\ g^{-1}$ soil	$\bar{x}$	24^{a}	44^{c}	36^{b}	17^{a}	24^{a}	14^{a}	<0.001
	SD	2.06	11.86	11.59	3.74	7.81	3.96	
Net mineralization mg N kg^{-1} day^{-1}	$\bar{x}$	-2^{c}	-2^{c}	-1^{b}	-1^{b}	0^{a}	0^{a}	<0.001
	SD	0.22	0.50	0.05	0.19	0.32	0.18	
Net nitrification mg N kg^{-1} day^{-1}	$\bar{x}$	0^{a}	0^{bcd}	0^{bcde}	0^{cdef}	0^{cdef}	0^{def}	<0.001
	SD	0.11	0.09	0.19	0.09	0.10	0.04	

a-f Means followed by different letters differ significantly ($P < 0.10$)

Soil moisture and N pools were highly variable across sites (Table 3.5). Soil moisture was highest in June (47 ± 7.1%) and was positively related to net mineralization (r = 0.63, $P = <$ 0.001, n = 30), unrelated to net nitrification ($P > 0.59$), and negatively related to leaching (r = -0.62, $P < 0.001$, n = 30). Aboveground plant N concentration in June was related to total soil mineral N (r = 0.38, $P = 0.04$, n = 30), soil moisture (r = 0.40, $P = 0.03$, n = 30), and June herbaceous root biomass (r = 0.41, $P = 0.03$, n = 30). Aboveground N concentration did not differ (ANOVA, $P = 0.683$) among plant groups (grass, forb, fescue, mixed species). June root length and biomass increased with soil moisture (r > 0.54, $P < 0.002$) as well as with soil NH_4-N (r > 0.44, $P < 0.02$, n = 30), while root diameters increased with soil moisture (r = 0.54, $P = 0.002$, and n = 30) but were unrelated to soil mineral N. June leaching of nitrates, indicated by the resin bags in the mineralization PVC cores, averaged 6 ± 4.08 µg/g resin across sites, which was approximately 11% of the average NO_3-N (56 µg/g) at the 5-cm soil depth, and 60% of the average NO_3-N at the 5-15 cm depth (11 µg/g). Nitrate leaching was negatively correlated with root biomass (r = -0.48 $P = 0.009$, n = 30) at the 0 -5 cm soil depth; the relationship at 5 - 15 cm depth could not be determined because root biomass was not measured at this depth.

June soil moisture (39 ± 6.7%), nitrate (56 ± 22.50 µg g^{-1} µ), and ammonium levels (52 ± 46.73 µg g^{-1}) dropped an average 17, 81 and 50% across sites by September (Table 3.6). While soil NH_4-N was positively related to soil moisture (r = 0.73, $P < 0.001$, n = 30) across sites in September, net nitrification was not related to soil moisture and NO_3-N declined with soil moisture (r = -0.66, $P < 0.001$, n = 30). High aboveground plant N concentration in September was associated with high soil NO_3-N (r = 0.69, $P < 0.001$, n = 30), but was unrelated to soil NH_4-N ($P = 0.21$) or total mineral N ($P = 0.54$) levels.

Aboveground plant N concentration in fall was negatively correlated with September root volume ($r = -0.44$, $P = 0.016$, $n = 30$). Root abundance (length and biomass) in fall was related to soil moisture ($r = 0.36$-0.50, $P < 0.05$, $n = 30$), unrelated to ammonium, and negatively related to NO_3-N ($r = 0.53$-0.68, $P < 0.003$, $n = 30$) while root diameter was related only to soil moisture ($r = 0.38$, $P = 0.04$, $n = 30$). Leaching was not measured in fall 2002.

There were no significant differences in net mineralization rate, net nitrification rate, relative net nitrification, leaching, or soil mineral N pools among clipping or grazing treatments (Table 3.6). Nitrates collected on resin bags (an indicator of leaching) tended to increase with frequency of clipping in spring. There were no significant treatment differences in N concentration or CN ratio in actively growing plant material above mineralization PVC cores. However, YR plots had higher total shoot N (g) in June and September than any of other treatments ($P < 0.010$) because YR plots had more actively growing biomass than all other plots (Table 3.6). There was evidence for an initial increasing trend in fall in the relative net nitrification with increasing clipping frequency.

3.3.5 Responses of individual rough fescue plants

Fourteen percent ($n = 21$ of 150) of plants could not be relocated over the course of the experiment. Of the remaining plants, nine (7%) died by August 2002. No marked plants produced seed-heads in 2002. There were no significant differences in percent mortality among the clipping treatments ($P = 0.45$). Similarly, after two years of clipping treatments there were no significant differences among treatments in above- and below-ground biomass, plant morphology or shoot N treatments across all sites (Table 3.7).

Table 3.6. Plant nitrogen (N), soil moisture, and mineral nitrogen in soils of fescue grasslands after 2 years of seasonal clipping treatments and natural grazing at the Ya Ha Tinda Ranch in southwestern Alberta, June and September 2002.

		June					September					*P*		
		Control	Winter	Winter Spring	Year-round	Grazed	Control	Winter	Winter Spring	Year-round	Grazed	S	T	SxT
Green shoot (g/core)	$\bar{x}$	0.104	0.121	0.086	0.141	0.091	0.138^{a}	0.105^{a}	0.144^{a}	0.188^{b}	0.067^{a}	0.382	0.024	0.691
	SD	0.048	0.041	0.058	0.090	0.019	0.093	0.083	0.080	0.120	0.033			
Shoot N (%)	$\bar{x}$	3.11	2.48	2.89	2.68	2.88	1.92	1.86	1.67	1.63	1.86	<0.001	0.262	0.298
	SD	0.44	0.26	0.57	0.54	0.46	0.32	0.37	0.28	0.27	0.36			
Shoot C (%)	$\bar{x}$	45.05	45.19	45.10	45.05	45.05	44.53	44.63	45.18	44.37	44.93	0.014	0.679	0.368
	SD	0.35	0.44	0.37	0.35	0.56	1.31	0.55	0.54	0.83	0.67			
Shoot CN ratio	$\bar{x}$	14.74	18.39	16.09	17.42	15.98	23.74	24.90	27.83	27.82	25.07	<0.001	0.407	0.522
	SD	2.06	1.98	3.11	3.66	2.54	3.85	5.64	5.34	4.93	5.82			
Total green shoot N (g)	$\bar{x}$	0.31^{a}	0.30^{a}	0.23^{a}	0.36^{b}	0.26^{a}	0.25^{a}	0.18^{a}	0.23^{a}	0.31^{b}	0.12^{a}	0.103	0.010	0.866
	SD	0.12	0.10	0.12	0.19	0.07	0.17	0.13	0.11	0.23	0.05			
Soil moisture (%)	$\bar{x}$	48.8	48.2	47.9	45.7	44.9	41.0	39.8	38.5	37.6	38.5	<0.001	0.878	0.955
	SD	7.57	7.98	6.69	8.54	5.35	8.95	6.13	5.91	7.02	7.12			
Ammonium N (μg g^{-})	$\bar{x}$	52	53	49	46	62	15	15	13	13	14	0.001	0.987	0.49
	SD	49.54	39.56	49.51	39.13	67.07	3.98	3.78	2.79	3.24	2.24			
Nitrate N (μg g^{-})	$\bar{x}$	54	51	60	67	50	8	7	7	9	8	<0.001	0.751	0.579
	SD	15.37	26.86	8.52	39.12	10.93	3.74	2.79	3.06	4.52	4.15			
Net Mineralization (mg N kg^{-1} day^{-1})	$\bar{x}$	2	2	1	2	2	-1	-1	-1	-1	-1	<0.001	0.805	0.997
	SD	1.63	0.96	2.27	2.45	1.20	0.91	0.60	0.61	0.67	0.66			
Net Nitrification (mg N kg^{-1} day^{-1})	$\bar{x}$	1	1	1	1	1	0	0	0	0	0	<0.001	0.812	0.880
	SD	0.62	0.51	0.49	0.39	1.20	0.26	0.29	0.21	0.24	0.13			
Relative net nitrification (%)	$\bar{x}$	64	58	80	53	123	-41	-49	0	-3	19	0.002	0.495	0.965
	SD	48.93	29.49	58.71	31.21	266.1	87.16	111.57	22.44	43.00	26.78			
NO_3 -N resin (μg g^{-1})	$\bar{x}$	6	6	6	7	8	NA	NA	NA	NA	NA		0.840	
	SD	3.28	3.52	2.48	5.92	5.22								
NH_4 –N resin (μg g^{-1}) soil	$\bar{x}$	1	1	1	1	1	NA	NA	NA	NA	NA		0.830	
	SD	0.30	0.32	0.27	0.28	0.60								

a-c Within a season and variable, means followed by different letters differ significantly ($P \leq 0.10$); NA, not available

Table 3.7. Morphological measures and mass (g/plant) of individual rough fescue plants after 2 years of seasonal clipping treatments and natural grazing at the Ya Ha Tinda Ranch harvested in August 2002.

		Control	Winter	Winter Spring	Year-round	Grazed	*P*
Final plant height (cm)	$\bar{x}$	17.93	15.12	13.36	7.84	8.80	0.129
	SD	11.48	8.30	8.48	6.15	4.91	
Basal area (cm^2)	$\bar{x}$	4.82	4.21	3.30	3.16	4.73	0.726
	SD	4.27	1.86	2.14	1.45	3.01	
Total tillers	$\bar{x}$	22.63	23.47	17.02	18.12	18.19	0.750
	SD	17.84	10.59	4.36	8.08	8.60	
Number green tiller	$\bar{x}$	17.03	16.40	9.39	11.83	13.13	0.690
	SD	15.69	8.71	5.89	6.75	7.50	
Aboveground biomass (g)	$\bar{x}$	1.709	1.044	0.483	0.246	0.319	0.318
	SD	2.723	1.191	0.415	0.264	0.261	
Aboveground green biomass (g)	$\bar{x}$	0.998	0.625	0.309	0.138	0.228	0.416
	SD	1.734	0.714	0.270	0.136	0.195	
Total aboveground annual production (g) *	$\bar{x}$	1.709	1.045	0.585	0.525	-	0.465
	SD	2.723	1.192	0.449	0.392		

* Production includes clipped biomass

3.4 DISCUSSION

After only two years, I found aboveground changes in plant biomass and composition with seasonal clipping and grazing, but I did not find the hypothesized reduction in roots that I expected at either the plot or individual plant level. However, the Ya Ha Tinda ranch experienced a severe drought in 2002, as defined by the Prairie Farm Rehabilitation Administration, representing the 0 – 10 percentile relative to historical precipitation (Agriculture and Agri-Food Canada 2003). As a consequence, the results of this study represent effects of defoliation on rough fescue during drought conditions.

As expected, standing aboveground biomass and the ratio of dead to live shoots decreased with frequency of clipping. These trends, while not always statistically significant, were consistent with previous studies that reported reduced yield in fescue grasslands when clipping or grazing was extended into the growing season (Johnson 1961, McLean and Wikeem 1985, Willms 1991), and the reduction was due primarily to declines in grass, including rough fescue (Bailey et al. 1987). For example, summer cattle grazing removed hard, deep-rooted, non-resistant grasses such as rough fescue in favor of less productive, shallow-rooted, and grazing-resistant grasses and forbs such as Parry oat grass (Danthonia parryi), slender wheatgrass (Agropyron trachycaulum), and shrubs, such as fringed sage (Artemesia frigida) (Dormaar and Willms 1990, Naeth et al. 1991, Willoughby 1992, Willms et al. 1996). In contrast, defoliation of fescue communities during the dormant season has not been found to reduce fescue production or tiller weight (Willms et al. 1986, Willms and Fraser 1992).

However, my results were not consistent with some findings of other studies. For example, Bailey et al. (1987) found that herbage production was stimulated with light spring grazing (35% of forage utilized) that was not evident in this study after two years. Similarly, lower spring and summer green biomass after winter clipping, compared to controls, in this study was not consistent with observations of Short and Knight (2003) who found that cattle grazing (50 to 90% forage utilization) in fall reduced green standing biomass the following spring but increased green standing biomass in summer. Further, Naeth et al. (1991) reported that canopy cover of live vegetation in fescue grasslands in August was greater on both lightly and heavily grazed pastures during the growing season than in ungrazed areas, whereas I found green herbage remained consistently higher on control plots than in clipped or grazed plots.

Higher total and green biomass on unclipped plots (controls) than on clipped or grazed plots in this study may be a short-term response resulting from initial grazing protection because standing dead vegetation after two years was relatively low at 5 of the 6 sites compared to other fescue grasslands (Johnston 1961, Willms et al. 1986, Naethe et al. 1991). Where accumulation of litter in ungrazed grasslands occurs, it initially may conserve moisture levels as a result of a change in microclimate from increased shade (Johnston 1961) or snowmelt moisture maintained under increased standing dead material (Dormaar and Willms 1990), but high accumulations of litter may result in reduced plant growth because of reduced light. If unclipped plots conserved moisture due to residual standing vegetation, drought effects may also have contributed to the unexpected levels of green biomass on control plots in 2002, when compared to other fescue studies.

I attribute the differences in biomass response primarily to the fact that controls in this study represent fescue communities that were in initial recovery from a recent history of heavy winter/spring and moderate summer grazing by elk. This view is supported by the lack of robustness of individual fescue plants that served as controls in this study compared to controls used in other fescue grasslands studies on similar soils and precipitation. For example, Willms et al. (1986) reported unclipped fescue plants that were 3 times the height (60 ± 1.9 cm) of the average control plants in this study (17.9 ± 7.3 cm) and tillers/plant (168 ± 37 cm) that were 8 times those observed in this study (22 ± 7.2). As a result, my comparisons indicate high removal of the aboveground biomass, even in the dormant season, is sufficient to reduce the rate of short-term recovery on fescue grasslands, although not as much as clipping or grazing continued during the spring and summer. This was particularly true for grass species including rough fescue, but not for forbs. However, I also cannot rule out effect of the drought in 2002 because forb cover was 40% lower in August of 2002 than 2001 (2001: 23.5 ± 9.19; 2002: 14.13 ± 5.65) and the forb response may be temporary.

Initial recovery in fescue grasslands resulted in an increase in the evenness of species present rather than a change in the number of species. This is in contrast to a number of studies that have examined the effect of cattle grazing on fescue communities protected for over 30 years, and have found that light to moderate grazing has increased both species number and diversity (Willoughby 1992). In these cases, grazing likely reduced tall, dominant plants and indirect effects of grazing such as modification of microclimate (Willms et al. 1986) and amount of photosynthetically active radiation (PAR) at the crown (Willms 1988) may be more directly influence plant responses.

Contrary to my expectation, belowground production did not significantly differ among clipping treatments. Several reasons may exist for the lack of differences in roots among treatments. First, root mortality and turnover may have occurred but dynamics occurred over a shorter or longer period, and my sampling interval was not sufficient to detect changes (Hamilton and Frank 2001, Frank et al. 2002). Hamilton and Frank (2001) found root turnover after clipping of *Poa pratensis* was evident in the first 24 hours after clipping but not after 7 days. In addition, dead roots were not removed from root biomass or length measurements from cores taken from the field. A 6-week greenhouse experiment on rough fescue defoliation (CHAPTER 4) indicated clipping decreased rough fescue root biomass. In the greenhouse, clipping effects may have been significant because the majority of living roots were harvested intact (from one plant) and residual dead roots were limited due to the short duration of the experiment. Alternatively, the 6-week study may have been too short to allow plants a period of recuperation and root reinvestment. Second, my experiment addressed short-term responses and effects large enough to detect differences within the variability across sites may take a number of years (Dormaar and Willms 1998).

Measures of soil mineral nitrogen were highly variable across sites and may have overwhelmed treatment differences. Similarly, recent research out of Yellowstone National Park indicated site variability had larger effects on soil properties than grazer effects (Verchot et al. 2002). In my study, shoot N (g) in green biomass increased with defoliation, but this was a result of increased living biomass, not N concentration (% N). Defoliation may have increased spring leaching, but leached nitrates were not a large percentage of the soil mineral N in this study. While not significant, defoliation tended to increase fall relative net nitrification. However, the 28-day mineralization trials may have been too long to capture the relationships among N-pools.

Soils may have been saturated during sampling periods; however this is common in montane fescue grasslands, particularly during the spring and fall when precipitation events are more common. In fact, Dormaar et al. (1984) reported spring soil moisture levels greater than 50% and fall soil moisture levels greater than 30% in the Ah horizon of grazed foothills fescue grassland, with moisture levels generally following seasonal precipitation patterns and absorption of snowmelt. In addition, Dormaar and Willms (1998) reported mean growing season soil moisture at 40% under light grazing (Ah horizon). While I did not find differences in soil moisture as a result of increased grazing intensity, decreased soil moisture has been reported in other studies for fescue grasslands (Johnston 1961), and is likely a result of decreased soil organic matter (SOM), increased bulk density, or decreased water infiltration (Dormaar and Willms 1990).

Nevertheless, aboveground grazing maintained vegetation in a young, N-rich condition and these changes may have implications for both forage selection and nutrient dynamics in rough fescue grasslands. For example, defoliation of individual rough fescue plants resulted in significant differences in shoot N (%) and total shoot N (g) by the end of the growing season. Total shoot N (g) decreased with defoliation, and this was due to decreased biomass at higher clipping frequencies. Differences in shoot N concentration and total shoot N of fescue under different clipping regimes presents a trade-off for grazing herbivores. Higher concentration of N, as observed under grazing, may be beneficial if biomass is great enough for efficient consumption. On the other hand, if biomass is so low that bite rate must increase, the lower quality fescue observed under no defoliation or winter defoliation may be more beneficial.

In conclusion, defoliation removed standing dead and increased the relative amount of green biomass available herbivores, and this effect was greater as defoliation continued into the growing season. A trade-off between dormant-season/early-spring clipping and year-round clipping occurs for grazing herbivores because while higher quality green plant material becomes more available under year-round defoliation, greater biomass and total shoot N result from defoliation that ceases earlier in the year. In addition, defoliation later into the growing season can decrease the percentage of rough fescue and plant community diversity and increase more grazing-tolerant, but less palatable, species such as shrubs and sedges. Maintenance of rough fescue under early spring clipping may indicate that fescue grassland can be sustained while grazed by migratory herbivores if defoliation stops before the cessation of vegetative growth. Even though bare ground increased under grazing, current herbivore numbers are not likely at levels that threaten sustainability as a result of hydrological changes and erosion. However, if herbivore numbers increase during the growing season, trampling of vegetation could become problematic. While differences in soil N-pools were not significant across treatments in the short-term, potential changes in relative net nitrification and leaching under growing-season grazing could result in N-loss from the system over the long-term. Further research on seasonal grazing in rough fescue grasslands should focus on the effects of defoliation on productivity, soil mineral N-pools, and rough fescue survival over a greater number of years. In particular, understanding of the grazing dynamics within fescue grasslands would increase from studies looking at root production and turnover and soil mineral N-pools at finer temporal scales during the growing season.

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CHAPTER 4

EFFECTS OF DEFOLIATION AND MINERAL N-FORM ON ROOT MORPHOLOGY AND GROWTH OF ROUGH FESCUE UNDER HIGH NITROGEN LEVELS

4.1 INTRODUCTION

Defoliation imposes a carbon limitation on plants by removing aboveground biomass and, in some systems, decreasing root biomass through root mortality (Thornton and Millard 1997, Arredondo and Johnson 1999). Defoliated grasses typically recover by allocating soluble C to shoots for photosynthetic recovery (Holland and Detling 1990, Arredondo and Johnson 1998, Paterson and Sim 2000) and, therefore, non-structural carbohydrates decrease in crowns and roots of defoliated plants (Thornton and Millard 1997, Skinner et al. 1999). As a result, nitrogen demands of defoliated grasses are high, relative to non-defoliated plants to support shoot regrowth under lower root biomass. However, field studies report higher mineral soil N and shoot N in grazed grasslands than ungrazed grasslands (McNaughton 1984, Polley and Detling 1988, Dormaar and Willms 1998, Baron et al. 2001). Feedback mechanisms for increasing soil N availability in grazed systems commonly include lower C:N values of grazed plant material, increased net N mineralization due to stimulated microbial activity from C flux in root exudates or root turnover, and input of animal excreta (Floate 1981, McNaughton 1985, Hobbs 1996, Detling 1998, Holland et al. 1996, Paterson and Sim 2000, Hamilton and Frank 2001).

Studies also have reported changes in the form of soil mineral N under grazing (Baron et al. 2001), with the ratio of inorganic NO_3-N to NH_4-N increasing approximately 2-fold with heavy grazing in rough fescue grasslands over time and a 2-5 fold increase seasonally (Dormaar and Willms 1998). Although reduction in denitrification could explain increases in NO_3-N, there is little evidence for reduced rates of denitrification with grazing (Ruz-Jerez et al. 1994, Luo et al. 1999). In fact, Frank and Groffman (1998b) found that large herbivores increased denitrification at mesic grassland sites by as much as 150%. However, Frank et al. (2000) reported that while grazers promoted denitrification, grazing reduced the denitrification to net mineralization ratio and this was likely the result of increased immobilization as indicated by a higher respiration:microbial C ratio on grazed sites. Alternatively, Jarvis and Barraclough (1991) have suggested that increased NO_3-N is due to autotrophic nitrifiers, which use NH_4-N as an energy source instead of carbon (Kaye and Hart 1997), and compete more successfully with plant and microbial uptake for NH_4-N when N inputs are high. In fact, Watson and Poland (1999) reported an increase in the proportion of NO_3-N over time in summer-grazed swards receiving high ($\geq$ 300 kg N ha^{-1} $year^{-1}$) fertilizer inputs, and this was a result of an increase in the nitrification rate. This fertilization rate is nearly equivalent to that of the standard estimate for ungulate urine hits (38 – 51 g N m^{-2}) (Stillwell 1983, Day and Detling 1990, Seagle et al. 1992, Hamilton et al. 1998, Wilsey 2002, Peek and Forseth 2003).

An increase in the relative amount of NO_3-N results in a soil more prone to leaching because NO_3-N is more mobile than NH_4-N (Robinson et al. 1994). However, in Yellowstone National Park, Frank et al. (2000) did not find increased leaching with ungulate grazing despite increased net mineralization and net nitrification, and suggested that grazers promoted N retention by stimulating microbial productivity related to increased labile C availability. And, Frank and Evans (1997) observed reduced plant δ^{15} N with grazing despite increased total plant N with grazing (Frank et al. 1994). They suggested that plants may have assimilated proportionally more NO_3-N than NH_4-N with grazing because the high net ammonification observed in grazed systems could increase nitrification and nitrification discriminates against δ^{15} NO_3-N. They hypothesized that plants in grazed systems may not need to invest as much in roots to support plant regrowth because NO_3-N is more mobile. Indeed, nitrate-based nutrition has been reported to increase shoot:root biomass in tomato plants (Bloom et al. 1993, Bloom 1997).

Consequently, grazing by large herbivores increases the heterogeneity of soil mineral N both in terms of distribution and form (Hobbs 1996). Afzal and Adams (1992) reported that up to 90% of consumed nitrogen is returned to the soil in concentrated patches via dung and urine and that mineral N varied spatially by up to 250 mg L^{-1}. Implications of patchy resources to plants have been studied in terms of plant competition (Robinson et al. 1999, Casper et al. 2000, Fitter et al. 2002); however, patchy resources may also affect the ability of plants to recover from defoliation. For example, grazing-sensitive species have been reported to increase root ramification and decrease specific root length and link length when defoliated (Arredondo and Johnson 1998, 1999). A decrease in link length with grazing is consistent with a shift in preference from NH_4-N, which depends upon root exploration, to NO_3-N, where absorption occurs more readily with inflow from the soil solution. Further, a decrease in specific root length may improve root longevity due to increased average diameter (Hendrick and Pregitzer 1992, Taub and Goldberg 1996, Arredondo and Johnson 1998, but see Sullivan et al. 2000). High hydraulic capacity and improved inflow associated with increased average root diameter may be important for efficient NO_3-N based nutrition (Sullivan et al. 2000, Wahl and Reyser 2000). For example, in a greenhouse experiment with wheat, Robinson et al. (1994) demonstrated that changes in root inflow, as opposed to root growth, were more important for nitrate capture.

To address the question of whether increased NO_3-N in soils of grazed systems may compensate for decreased root biomass in defoliated plants (Robinson et al. 1994), I conducted a greenhouse experiment to determine whether N uptake and plant regrowth of rough fescue increases more under high NO_3-N than NH_4-N availability, and whether shifts in root morphology and survival are associated with improved plant regrowth after defoliation. I used rough fescue (*Festuca campestris*) because it is sensitive to growing season grazing (Johnston 1961, Willms et al. 1985, Chapter 3) and inorganic NO_3-N is known to increase relative to NH_4-N in rough fescue grasslands with grazing (Dormaar and Willms 1998). I hypothesized that although root and shoot biomass of fescue plants would decline with defoliation, plant N uptake per g root would increase with high NO_3-N fertilization compared to NH_4-N fertilization resulting in improved regrowth, and this is associated with increased root diameters, lower root branching, and higher root survival rates.

4.2 MATERIALS AND METHODS

4.2.1 Experimental conditions and species

Rough fescue seeds (Bedrock Seed Company, Edmonton, Alberta) were planted and germinated in MetroMix in an environmental chamber under 18 hours of daylight (20:10C) (Willms 1988). After 2 weeks, seedlings (n = 50) were standardized by tiller number (n= 3-4), placed in 6L plastic pots (Jackson and Caldwell 1989, Crabtree and Berntson 1994, Fransen et al. 1999), and grown in a mixture of soil (approx. 4.3L) collected on at the Ya Ha Tinda Ranch, west of Sundre, Alberta (20 cm depth), sieved topsoil available at the University of Alberta, and perlite (~ 4:6:4). Pots were modified as in Pärtel and Wilson (2001) to accommodate a 6-cm clear plastic minirhizotron tube placed 5 cm below the soil surface horizontally through 6 adjacent pots. Within each pot, the acryclic tube was divided into 13 imaging frames (13.5 x 13.5 mm) using the standard BTC indexing handle available with the BTC I-CAP image capture system (Bartz Technology Corporation, Santa Barbara, California, USA). Black electrical tape was wrapped around portions of the minirhizotron tube that were outside the pots to inhibit light penetration (Pärtel and Wilson 2001). Plants were watered to approximately 80% field capacity and monitored weekly for visible root growth by collecting 13 root images from within each pot.

Twelve weeks after transplanting (10 October 2002), experimental treatments were initiated on 14-week old seedlings. Ten plants were harvested immediately to measure initial plant and soil conditions. The remaining plants (n = 40) were subjected to one of two fertilizer treatments (NH_4-N or NO_3-N) and to one of two clipping treatments (Unclipped or Clipped) in a 2-factorial design. Plants were fertilized with either NO_3-N (consisting of KNO_3 and $Ca(NO_3)_2$) or NH_4-N ($(NH_4)_2SO_4$) (Bailey 1998). KNO_3 and $(NH_4)2SO_4$ were isotopically labeled at 5 atom % ^{15}N abundance, resulting in 5 % atom ^{15}N fertilizer supplied to the NH_4-N treatment and 1.67 % atom ^{15}N fertilizer in the NO_3-N treatment. Fertilizer was isotopically labeled in order to trace the form of nitrogen taken up by the plants. Plants were fertilized 3 times a week, for 6 weeks, and received 0.945 g N pot^{-1} (300 kg ha^{-1}) over the course of the experiment. This fertilization rate is nearly equivalent to that of the standard estimate for ungulate urine hits (38 – 51 g N m^{-2})

(Stillwell 1983, Day and Detling 1990, Seagle et al. 1992, Hamilton et al. 1998, Wilsey 2002, Peek and Forseth 2003). A modified, N-free Hoagland solution was added to ensure other nutrients were not limiting plant growth (McCrimmon and Karnok 1992, Crabtree and Berntson 1994, Wahl and Reyser 2000). Care was taken to distribute fertilizer slowly and evenly over the entire surface area of the soil. Plants were clipped to 4 cm at the start of the experiment and 3 weeks after the experiment began. All plants were harvested 6 weeks after the beginning of the experiment.

4.2.2 Plant measurements

Aboveground morphologic and demographic measurements collected prior to each clipping and before the final harvest included total plant height, number of tillers, number of dead tillers, and basal area. On each plant, 3 tillers were arbitrarily selected and the height of each marked tiller was recorded as an indication of photosynthetic capacity.

Minirhizotron images of root window frames were collected prior to clipping (week 1), 7 days after the first clipping (week 2), 7 days after the second clipping (week 4), and just before harvest (week 6). Root images from 8 frames in the center of each pot were digitized using Rootracker software version 2.0 (David Tremmel, Duke University, Durham, North Carolina, USA). Root parameters measured included: number of live roots, total root length/sampling frame, root volume, mean root segment diameter and root branching order (Fitter 1986, Fitter and Stickland 1992, Taub and Goldberg 1996). If lateral branches were not observed on a root within a frame, the root was classified as an "apparent 1st order root" and root order classification increased with each increase in lateral branching (Wells et al. 2002). Roots were considered dead if they disappeared or shriveled and blackened (Wells and Eissenstat 2001). The presence of root hairs was also recorded for each root segment.

After each clipping, and at harvest, aboveground material was separated into shoots and crowns, oven dried at 50° C for 48 hours, and weighed. Plant material was ground to a fine powder in a ball grinder, and analyzed for total % N content with a Carlo-Erba Autoanalyzer NA1500 by the Renewable Resources Stable Isotope Lab at the University of Alberta (Tabatabai and Bremner 1991). Atom % 15N of plant material was measured using a VG SIRA 10 Mass Spectrometer attached to the autoanalyzer at the University of Alberta (Pruden et al. 1985).

Belowground crowns and roots were extracted from pots by hand and sieved (4 mm) to collect soil clinging to roots (rhizosperic soil). The remaining soil (bulk soil) was sieved to collect any additional roots and to collect an homogenous sample of soil. Rhizospheric and bulk soils were immediately frozen (-18° C) until N analyses could be conducted. Belowground crowns and roots were stored at 4° C for less than 7 days until processed in the lab. Roots were briefly floated in deionized water (< 30 min) to remove belowground crowns, residual soil and perlite, dried at 50° C for 48 hours, and weighed. Root material was ground and analyzed for N concentration and atom % 15N as described above.

Soil samples were analyzed for total N, NO_3-N, NH_4-N, atom % 15N of total N, atom % 15N of NO_3-N, and percent soil moisture. Atom % 15N of NH_4-N was not analyzed because it was at trace levels in the soil by the end of the experiment. Total soil N and atom % 15N of soil N were analyzed in the same manner as plant material described above. Mineral N (NO_3-N, NH_4-N) was measured by shaking 10 g (oven-dry equivalent) of field moist soil with 50 mL of 2 mol/L KCl for 30 min and filtering through, VWR brand 410, filter paper (Maynard and Kalre 1993). Extractant was frozen in vials (-18° C) and analyzed with a Technicon Autoanalyzer II (Industrial Methods #90-70 and #100-70W-B, Technicon Industrial Systems, October 1973) by the Renewable Resources High Volume Lab at the University of Alberta. Soil extracts were prepared for atom % 15N analyses using the diffusion method as described by Brooks et al. (1989) and analyzed by the Renewable Resources Stable Isotope Lab at the University of Alberta.

4.2.3 Mathematical and statistical analyses

The percentage uptake of 15N (%U) by plants from either the labeled NH_4-N or NO_3-N fractions in the fertilizer were calculated following Bailey (1999) as:

$$\%U = \frac{\text{atom \% excess in samples}}{\text{atom \% excess in fertilizer}} \; x \; \frac{\text{yield of N (mg per pot) in samples}}{\text{fertilizer application (mg per pot)}}$$

Differences in final plant and soil values from plants among clipping and fertilizing treatments were analyzed using a GLM univariate factorial analysis in SPSS 11.5 (SPSS Incorporated, Illinois, USA), with a significance value of $\alpha = 0.05$. The estimated mean squares were calculated using the Type III sums of squares error term. Pearson correlations were used to test relationships between variables. Temporal changes in above- and belowground morphology and abundance of root segments were tested using a GLM procedure with repeated measures in SAS (SAS Institute, Inc, Cary, North Carolina, USA).

The mid-point in the time interval prior to its observation in the minirhizotron imaging sessions was used as the date of birth and death, which assumed an even distribution of births and deaths between observations (Hooker et al. 2000). I modeled birth rates (first appearance) associated with clipping and N-form treatments with a Poisson regression analysis (POISSON: Intercooled Stata 7.0, Stata Corporation, Texas, USA) using the counts of new segments during each time period. I used a Cox proportional hazards regression (STCOX: Intercooled Stata 7.0, Stata Corporation, Texas, USA) to model the effects of clipping and fertilizing treatments, root morphological measures, cohort (when roots first appeared) and their interactions on longevity of root segments. The proportional hazards model takes the form:

$$h_i(t) = h_0(t)\exp(\beta_1 x_{i1} + ...\beta_k x_{ik})$$

where $h_i(t)$ defines the hazard of an individual root segment at time, t, as the product of a baseline hazard function and a linear function of k covariates. I used right-censored data, since not all roots died by end of the experiment, and incorporated different entry times using the Anderson et al. (1993) modification because roots appeared (birth) at different times in the experiment. Morphological root measurements used in the analysis were associated with the interval of exposure taken in imaging session at the beginning of the exposure interval. Individual root segment length was not included in the survival analyses because roots could extend into adjacent frames and total individual root length could not be calculated.

I report the hazard ratio (e^{β}) where (e^{β}-1) x 100 gives the percent change in the hazard of mortality related with 1-unit increase in the covariate keeping all other variables constant. A hazard ratio < 1.0 indicates that an increasing value of the covariate is associated with a decreasing risk of mortality. For a dichotomous variable, the hazard ratio is the ratio of the hazard for roots with a value of 1 compared to the hazard of the standard (0) (Allison 1995). I evaluated the proportional hazards assumption based on the distribution of the Schoenfeld residuals. Because root segments (n= 2027) observed extended into the adjacent sampling frame, I conducted the survival analysis with roots labeled as "extending into" or "continuing from" other frames and without these segments.

4.3 RESULTS

4.3.1 Plant growth and demography

Clipping removed 20 ± 0.08 percent of the aboveground growth and resulted in reduced above- ($P < 0.001$) and belowground ($P < 0.001$) biomass of rough fescue (Fig. 4.1) at the end of the experiment. On average, clipping reduced aboveground production by 41% ($P = 0.003$) and root biomass by 70% ($P < 0.001$). Lower shoot biomass in clipped plants at the end of the experiment resulted from fewer tillers being produced, rather than increased tiller mortality (Table 4.1). Individual tillers were lighter due to removal of shoot biomass with clipping. The decline in tillers was not reflected in reduced plant basal area by the end of the experiment, but clipping resulted in rough fescue plants that were 24% shorter at the end of the experiment (Fig. 4.2). In contrast, N-form influenced only aboveground biomass ($P = 0.002$, Fig. 4.1), and there were no significant clipping x fertilization interactions (Table 4.1). N-form had no effect on plant height, basal area or tillering (Table 4.1).

Over the course of the experiment, root length and diameter increased while the root order and the percentage of roots with root hairs initially declined, and then increased (Fig 4.3, Table 4.2). The increase in root length (mm) observed in a sampling frame was slower with clipping and the difference was exaggerated over time (time x clipping interaction: Table 4.2). In contrast, changes in root diameter and order were similar among the clipping treatments. The proportion of roots with root hairs did not increase as quickly in clipped plants as in control plants after their initial decline, but the increase was faster in the NO_3-N than the NH_4-N treatment (time x clipping x N-form interaction). N-form had no other effect on root morphology.

Risk of individual root segment mortality was significantly related to root diameter, total root length within a frame, root order and both N-form and clipping treatments (Table 4.3). For every additional mm in root width, roots had a 79% lower risk of mortality; an increase in root order resulted in a 17% greater risk of mortality (Fig. 4.4). Mortality of root segments decreased with increasing total root density. Risk of root mortality declined 29% on average in the NH_4-N treatment, while clipping reduced the risk of mortality on average by 15%.

Root segment appearance declined 2.5% per day over the course of the experiment (Table 4.4). In contrast to root mortality, appearances of roots decreased 22% with clipping and increased 12% with the application of NH_4-N and there was no interaction.

4.3.2 Soil mineral N pools and plant N uptake

At the start of the experiment, soil in the pots had an average of 106 ± 42.30 μg NO_3-N g^{-1} soil and 4 ± 0.69 μg NH_4-N g^{-1} soil and soil moisture averaged $27.8 \pm 3.61\%$ (n = 10). By the end of the experiment, N-fertilization had increased mineral N over 4-fold, with average soil NO_3-N increasing to 493 ± 85.39 μg g^{-1} soil and average soil NH_4-N to 6 ± 5.30 μg g^{-1} soil (n=40). Soil moisture decreased only slightly to $24.5 \pm 6.80\%$ (55 ± 15 % field capacity).

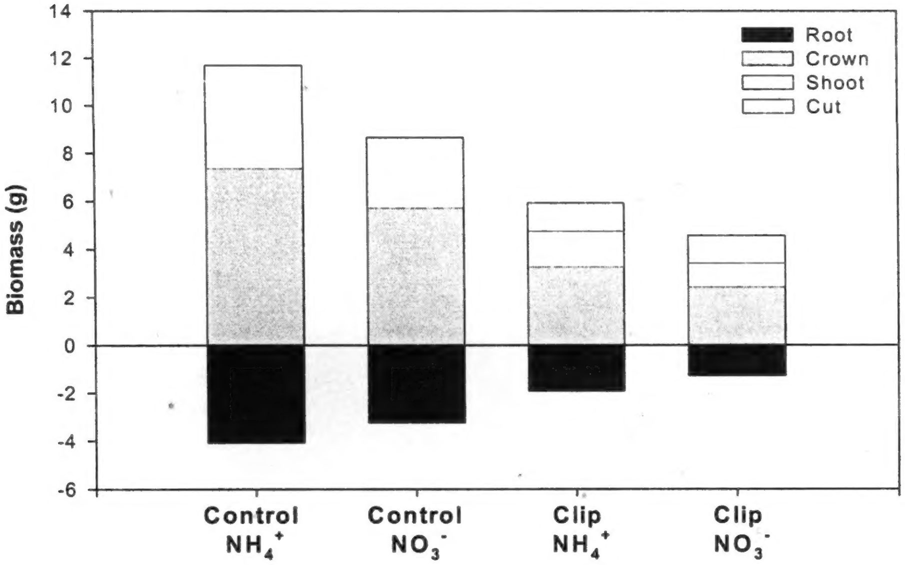

Fig. 4.1. Above- and belowground biomass of *Festuca campestris* after 6 weeks of N-form and clipping treatments.

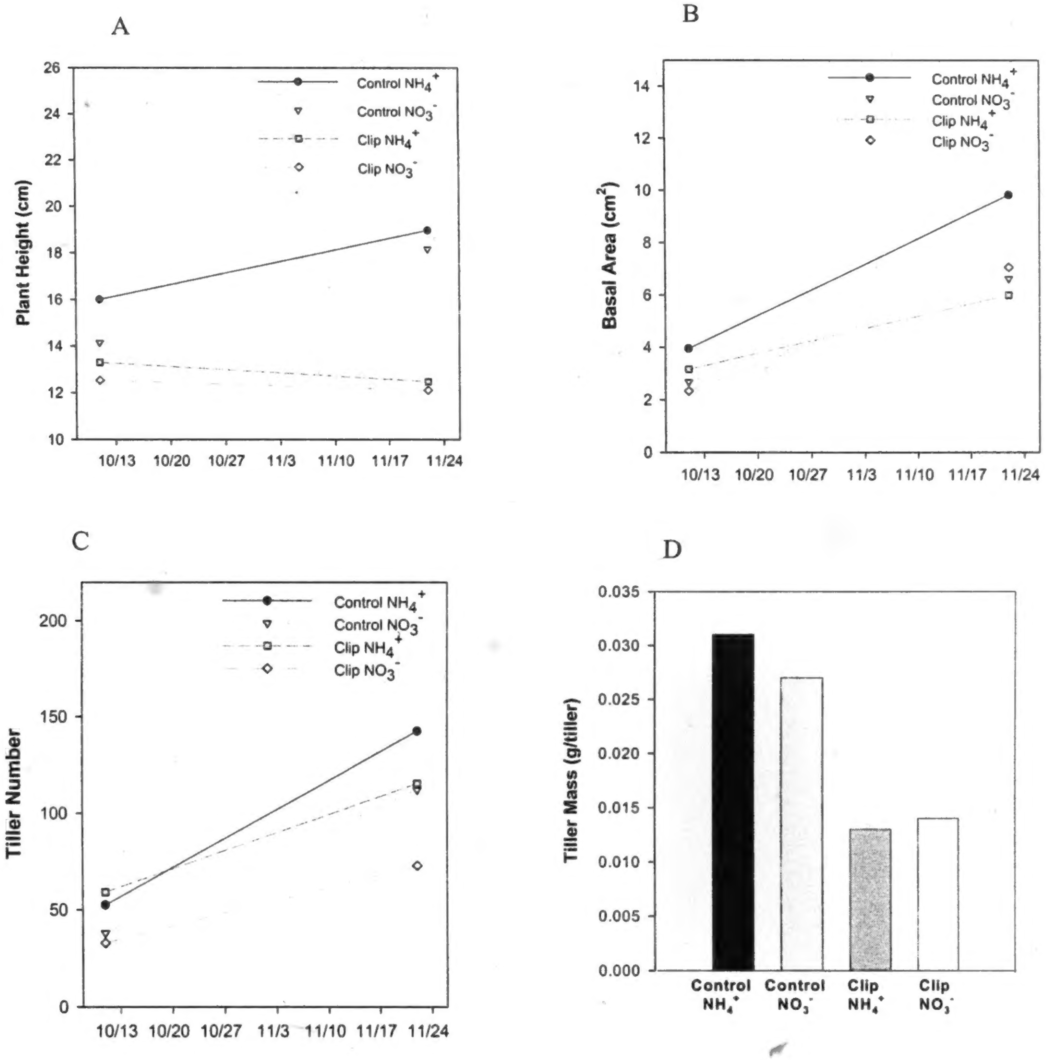

Fig. 4.2. Changes in morphological characteristics of fescue plants within clipping and N-form treatments over the course of the experiment (A-C) or at the end of the experiment (D).

Table 4 1. Main effects and interactions of clipping and N-form treatments on the difference in shoot morphology at the beginning and end of the experiment.

Variable	df	Type III SS	F-value	*P*
Plant height				
Clipping	1	169.74	24.27	0.00
N-form	1	5.33	0.76	0.39
Clipping x N-form interaction	1	1.09	0.16	0.70
Error	36	251.81		
Average tiller height				
Clipping	1	95.17	13.31	0.001
N-form	1	8.93	1.25	0.27
Clipping x N-form interaction	1	4.69	0.66	0.42
Error	36	257.43		
Basal area				
Clipping	1	12.66	0.42	0.52
N-form	1	0.002	0.00	0.99
Clipping x N-form interaction	1	36.29	1.21	0.28
Error	36	1077.85		
Dead tiller				
Clipping	1	180.63	0.74	0.40
N-form	1	765.63	3.15	0.09
Clipping x N-form interaction	1	87.03	0.36	0.55
Error	36	8759.70		
Green tiller				
Clipping	1	8850.63	10.22	0.003
N-form	1	525.63	0.61	0.44
Clipping x N-form interaction	1	99.22	0.12	0.74
Error	36	31189.30		
Tiller number				
Clipping	1	11560.00	18.78	0.00
N-form	1	2560.00	4.16	0.05
Clipping x N-form interaction	1	0.40	0.001	0.98
Error	36	22161.20		

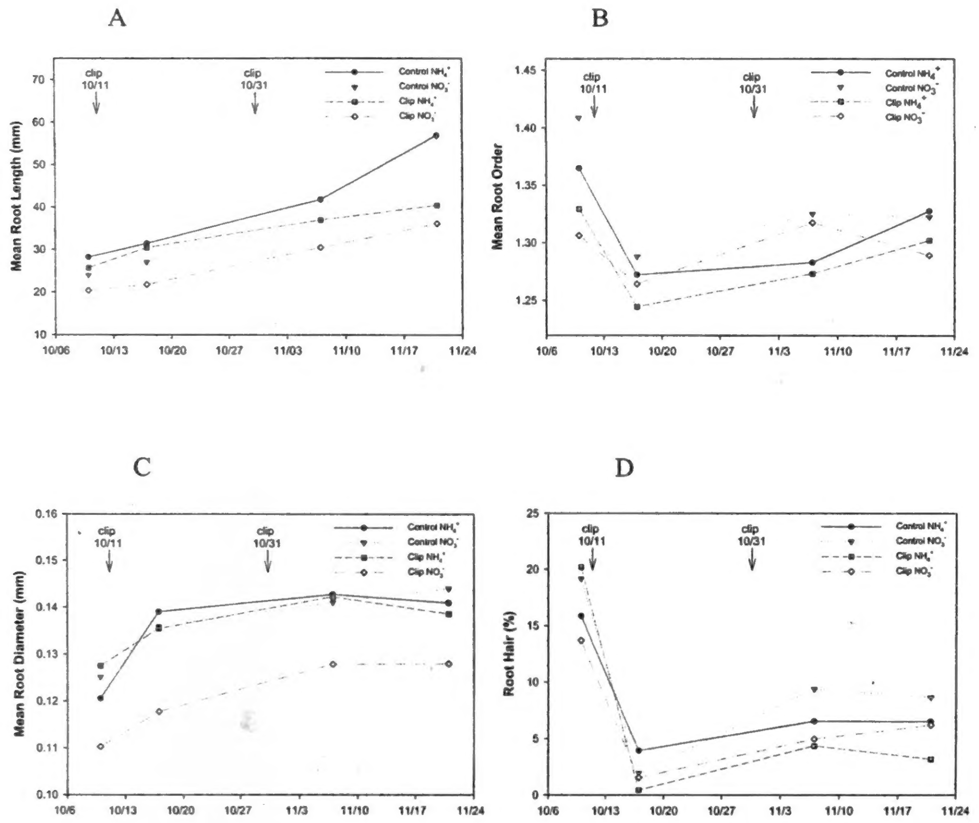

Fig. 4.3. Changes in (A) mean root length (mm/frame), (B) mean root order, (C) root diameter (mm) and (D) percent of roots with root hairs by clipping and N-form treatments during the 42-day experiment.

Table 4.2. Repeated measures main effects and interactions of clipping and N-form treatments on root morphology measured at four sampling dates.

Variable	df	Type III SS	F-value	*P*
Root length				
Between subject effects				
Clipping	1	3216.94	3.97	0.05
N-form	1	981.93	1.21	0.28
Clipping x N-form interaction	1	61.71	0.08	0.78
Error	36	29181.04		
Within subject effects				
Time	3	13560.99	100.64	<0.001
Time x clipping	3	1665.27	12.36	<0.001
Time x N-form	3	115.88	0.86	0.46
Time x clipping x N-form	3	30.80	0.23	0.88
Error	108	4850.95		
Root diameter				
Between subject effects				
Clipping	1	0.002	0.54	0.47
N-form	1	0.002	0.46	0.50
Clipping x N-form interaction	1	0.002	0.55	0.46
Error	36	0.16		
Within subject effects				
Time	3	0.008	21.35	<0.001
Time x clipping	3	0.0003	0.72	0.54
Time x N-form	3	0.0002	0.62	0.60
Time x clipping x N-form	3	0.0001	0.35	0.79
Error	108	0.01		
Root order				
Between subject effects				
Clipping	1	0.04	1.11	0.30
N-form	1	0.01	0.24	0.62
Clipping x N-form interaction	1	0.003	0.08	0.79
Error	36	1.43		
Within subject effects				
Time	3	0.15	6.98	0.0002
Time x clipping	3	0.02	0.92	0.43
Time x N-form	3	0.01	0.66	0.58
Time x clipping x N-form	3	0.01	0.40	0.75
Error	108	0.76		
Root hairs				
Between subject effects				
Clipping	1	0.16	5.10	0.03
N-form	1	0.01	0.22	0.64
Clipping x N-form interaction	1	0.00	0.00	0.98
Error	36	1.15		
Within subject effects				
Time	3	2.08	83.98	<0.001
Time x clipping	3	0.03	1.15	0.33
Time x N-form	3	0.06	2.31	0.08
Time x clipping x N-form	3	0.10	3.92	0.01
Error	108	0.89		

Table 4.3. Coefficients of Cox proportional hazards regression of individual root segments of *Festuca campestris* grown in pots and subjected to clipping (clipped/unclipped) and nitrogen form (ammonium/nitrate) treatments. No clipping and ammonium treatments are standards in dichotomous variables.

	Hazard ratio	Std. Error	Z	*P*	Upper Confidence Limit	Lower Confidence Limit
Clipping	0.8491	0.0419	-3.31	0.001	0.7708	0.9354
Nitrogen form	1.2854	0.0626	5.16	0.000	1.1684	1.4141
Root diameter (mm)	0.2136	0.0717	-4.60	0.000	0.1106	0.4123
Root length[1] (mm)	0.8712	0.0096	-12.48	0.000	0.8525	0.8903
Root order	1.1651	0.0522	3.41	0.001	1.0672	1.2719

[1] Total root length in surrounding frame

Table 4.4. Coefficients of Poisson regression analysis of counts of new roots appearing over time as a function of clipping and N-form treatments. No clipping and ammonium application are standards in dichotomous variables.

	Incidence rate ratio	Std. Error	Z	*P*	Lower Confidence Limit	Upper Confidence Limit
Days	0.975274	0.000732	-33.38	0.001	0.973841	0.976709
Clip	0.782602	0.014281	-13.43	0.001	0.755106	0.811100
N-form	0.884253	0.016046	-6.78	0.001	0.853356	0.916269

Table 4.5. Mean ± standard deviation of soil and plant nitrogen values, and statistical results for main effects and interactions of two experimental N-form (F) treatments and 2 clipping (C) treatments.

	Control	Control	Clip	Clip	*P*		
	NH4	NO3	NH4	NO3			
Variable	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	C	F	C x F
Soils							
Soil NO$_3$-N (ug/g)	445 ± 47.43	458 ± 51.70	552 ± 102.97	519 ± 86.76	0.001	0.688	0.352
Soil NH$_4$-N (ug/g)	13 ± 7.13	3 ± 0.29	4 ± 0.65	3 ± 0.34	0.001	0.000	0.001
Soil moisture (%)	19.6 ± 4.21	19.8 ± 4.89	30.9 ± 5.73	27.7 ± 4.20	0.000	0.322	0.270
Total N (g m^{-2})	601 ± 29	597 ± 19	600 ± 7	600 ± 13	0.892	0.787	0.787
Mineral N (g m^{-2})	37 ± 4	37 ± 4	45 ± 8	42 ± 7	0.002	0.532	0.447
Organic N (g m^{-2})	564 ± 29	560 ± 17	555 ± 10	558 ± 15	0.357	0.949	0.613
Plant N (%)							
Shoot N (%)	2.08 ± 0.20	2.16 ± 0.18	2.20 ± 0.25	2.26 ± 0.21	0.114	0.266	0.883
Crown N (%)	1.64 ± 0.14	1.53 ± 0.16	1.76 ± 0.25	1.68 ± 0.24	0.048	0.171	0.814
Root N (%)	1.88 ± 0.18	1.74 ± 0.15	1.57 ± 0.19	1.48 ± 0.15	<0.001	0.050	0.752
Shoot N (g)	0.09 ± 0.02	0.06 ± 0.02	0.03 ± 0.01	0.02 ± 0.01	0.000	0.002	0.175
Cut N (g)	0 ± 0	0 ± 0	0.03 ± 0.02	0.03 ± 0.04	0.000	0.891	0.891
Crown N (g)	0.04 ± 0.02	0.03 ± 0.02	0.02 ± 0.02	0.01 ± 0.01	0.002	0.149	0.855
Root N (g)	0.09 ± 0.02	0.06 ± 0.03	0.02 ± 0.01	0.02 ± 0.01	0.000	0.015	0.226
Total Plant N (g)	0.21 ± 0.056	0.15 ± 0.06	0.07 ± 0.04	0.05 ± 0.03	0.000	0.012	0.278
Shoot N/g root	0.027±0.068	0.027±0.011	0.062±0.0243	0.057±0.019	<0.001	0.630	0.583
% Utilization 15 N							
Plant N	16.65 ± 4.37	14.00 ± 5.94	6.80 ± 3.72	5.86 ± 5.47	<0.001	0.260	0.590
Shoot N	6.62 ± 2.15	5.39 ± 2.18	2.36 ± 1.08	1.83 ± 1.06	<0.001	0.112	0.521
Cut N			1.10 ± 0.77	1.44 ± 2.30		0.665	
Crown N	4.81 ± 2.54	3.67 ± 1.86	2.24 ± 2.00	1.82 ± 2.41	0.003	0.275	0.615
Root N	5.22 ± 1.77	4.94 ± 3.66	1.11 ± 0.64	0.78 ± 0.66	<0.001	0.647	0.970
Soil N	99.68 ± 12.30	104.16 ± 11.28	107.29 ± 16.98	102.08 ± 16.14	0.548	0.937	0.294
Mineral Soil N	63.24 ± 16.19	88.74 ± 31.95	88.41 ± 19.96	86.37 ± 18.92	0.119	0.109	0.062
Organic Soil N	36.44 ± 7.71	15.42 ± 33.15	18.87 ± 8.02	15.70 ± 6.56	0.133	0.038	0.121
Total	116.33 ± 11.83	118.18 ± 13.17	114.09 ± 13.99	107.94 ± 14.20	0.148	0.612	0.350

Inorganic nitrate remaining in the soil at plant harvest averaged 16% higher under clipped plants, while soil NH_4-N was 51% lower under clipping (Table 4.5). High nitrate in soils of clipped plants at the end of the experiment was associated with high soil moisture (r = 0.744, P < 0.001, n = 40). There was a drop in soil ammonium under clipping and NH_4- N application that was not evident when plants were not clipped (N-form x clipping interaction: Table 4.5). Soil mineral N increased with clipping and was inversely related to the total amount of N that accumulated in plant biomass (r = -0.660, *P* < 0.001, n = 40). There were no significant differences in total soil N or organic soil N among treatments.

Although clipping reduced nitrogen concentrations of roots, it did not reduce shoot or crown N concentrations, probably due to excess N in the system (Table 4.5). While total N (g) in shoots was lower because of reduced biomass with clipping, nitrogen accumulated aboveground/root (g/g) at harvest was higher (Table 4.5). In addition, plant N uptake/root (g/g) was positively associated with decreased root branching (r = -0.386, *P* = 0.019, n = 40) but not increased root diameter (*P* = 0.610). Even though most N in the experiment was nitrified, root nitrogen concentration and root and shoot N accumulated at harvest was higher under the NH_4-N treatment (Table 4.5).

The total percent recovery of ^{15}N-labelled fertilizer in the experiment did not differ among treatments (Table 4.5). Most of the fertilizer (90 ± 6%, n = 40) was retained in the soil. Of the ^{15}N in the soil, 82% of ^{15}N-labelled fertilizer remained in mineral form by the end of the experiment (Fig. 4.5). There were no significant treatment differences in the percent recovery of ^{15}N in the total N or mineral N in the soil (Table 4.5). However, the percent utilization of labeled fertilizer increased by 44% in the soil

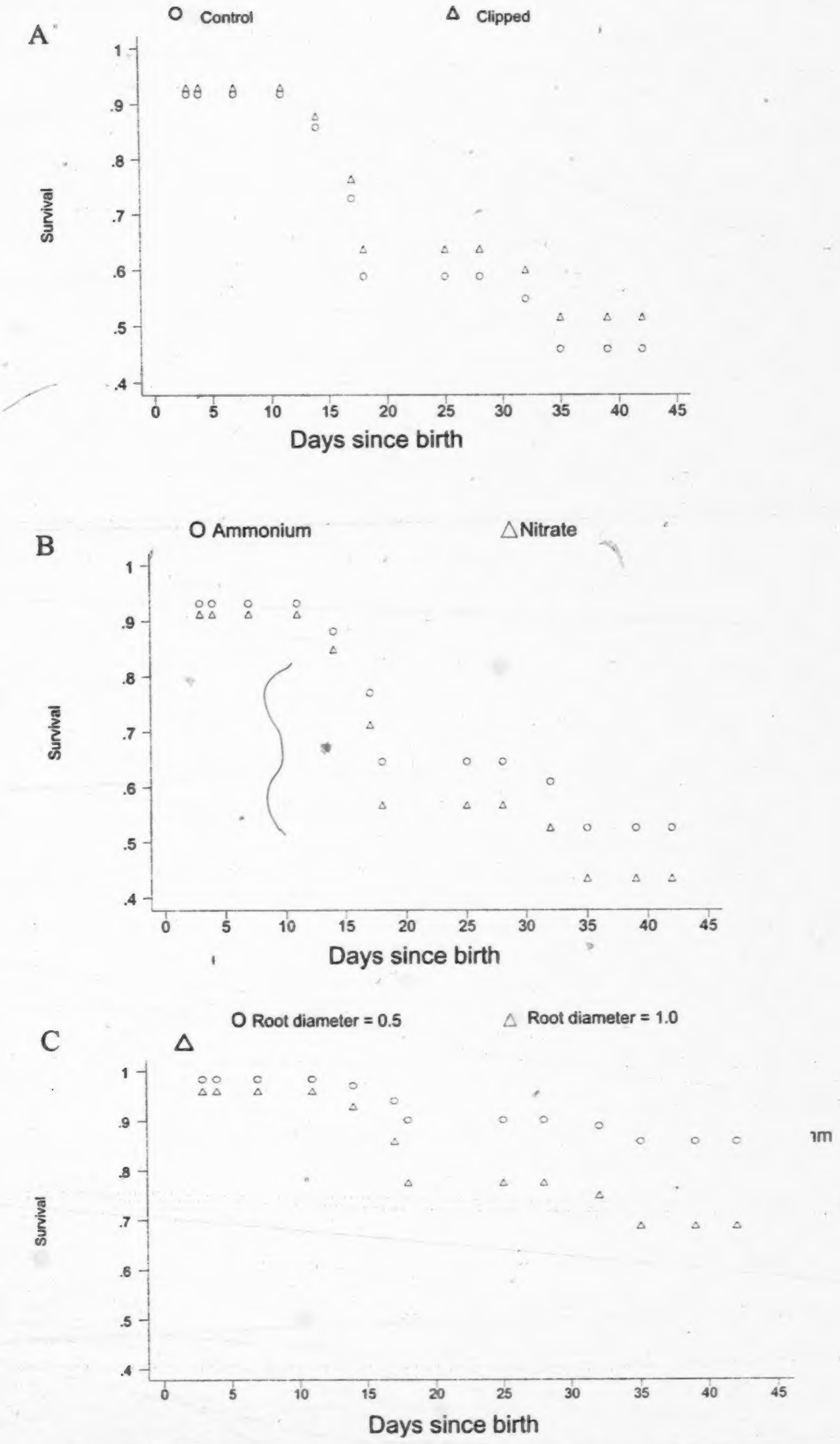

Fig. 4.4. Survival probabilities for *Festuca campetris* under (A) different clipping treatments, (B) different N-form treatments, and (C) comparing influence of two example root diameters.

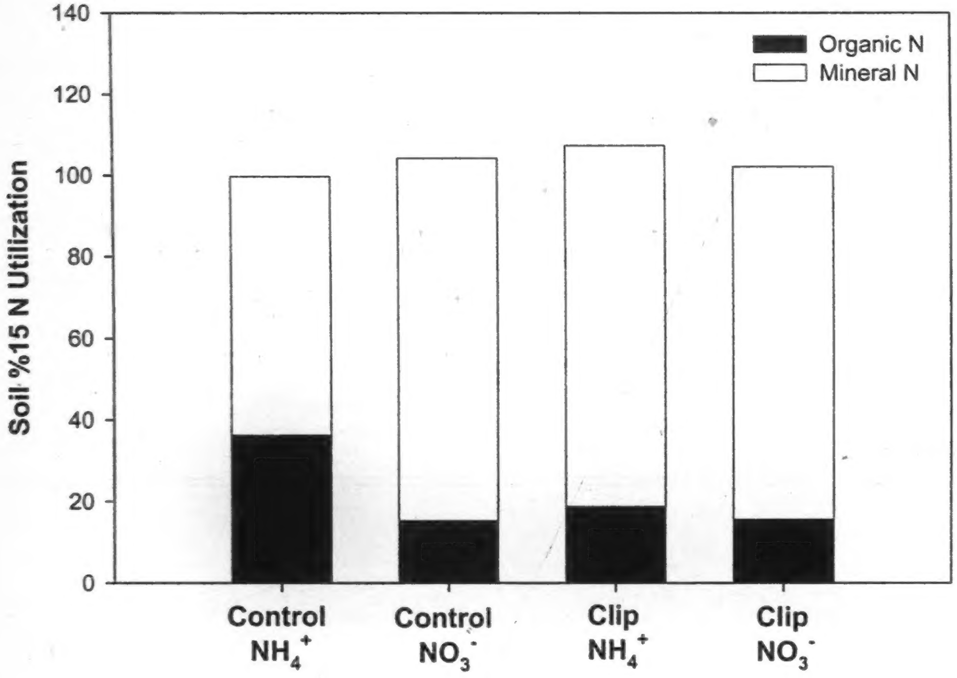

Fig. 4.5. Percent utilization of ^{15}N-labelled fertilizer in soils under *Festuca campestris* after 6 weeks of N-form and clipping treatments.

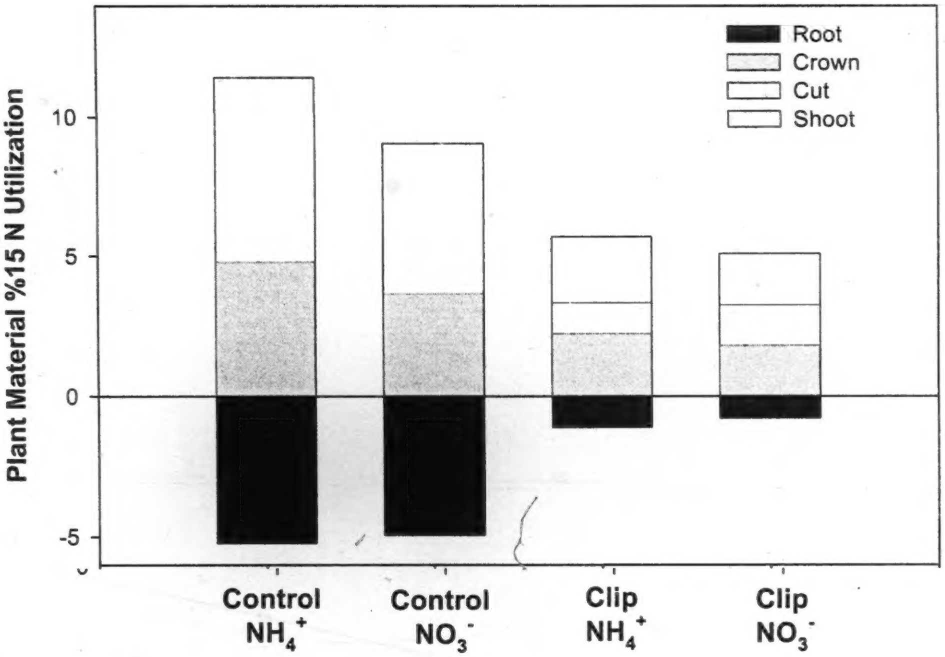

Fig. 4.6. Percent utilization of 15N-labelled fertilizer in *Festuca campestris* plant material after 6 weeks of N-form and clipping treatments.

organic N of plants fertilized with NH_4-N ($P = 0.038$, Fig. 4.6). In contrast, mean percent utilization of ^{15}N in plants decreased by 59% with clipping but not with N-form. This effect was consistent across shoots, crowns, and roots (Table 4.5), although the majority of plant ^{15}N uptake was in the shoots (Fig. 4.6).

4.4 DISCUSSION

Because a nitrification inhibitor was not utilized in this experiment, the majority of NH_4-N fertilizer was nitrified. As a result, I could not test for differences resulting from NH4-Nand NO3-N treatment effects as originally intended. Instead, the two treatments likely represent a nitrate and a mixed nutrition fertilizer. The mixed nutrition occurred because I continually added NH4-N fertilizer, which was subsequently nitrified, to soils in the experiment that were initially dominated by NO3-N. Thus, I discuss my results in light of these potential effects.

Clipping reduced above and belowground biomass of rough fescue at the end of the experiment and fertilizer did not influence plant recovery as hypothesized. The reduction in aboveground biomass with defoliation resulted from biomass removal and low tillering rates, while reduction in belowground biomass resulted from decreased root births and slower root elongation, rather than increased root mortality. Fescue is known to be grazing sensitive and aboveground biomass and basal area have been found to decrease with heavy defoliation (Johnston 1961, McLean and Wikeem 1985, Willms et al. 1998, and King et al. 1998, Chapter 3). Similarly, declines in rough fescue roots have been reported in both clipping and grazing studies (Johnston 1961, McLean and Wikeem 1985, Willms et al. 1998, and King et al. 1998), but declines are often attributed to mortality, rather than reduction in root appearances. To my knowledge this is the first study that has reported reductions in root production of rough fescue as a result of defoliation.

In contrast, field studies by Frank et al. (2002), who measured monthly root extension in minirhizotron tubes on grasslands dominated by *Pseudoroegnaria spicata*, *Festuca idahoensis, Deschampsia caespitosa*, *Poa pratensis*, or *Agropyron cristatum* in Yellowstone National Park, reported that grazers stimulated net belowground production by 35% and root mortality by 22%. However, Frank et al.'s (2002) measures of belowground production and mortality (initial root biomass x mean seasonal change from initial condition) may reflect initial root differences that have accumulated over time, whereas I directly show patterns in birth and survival of individual root segments in time. The authors suggested increased productivity may have occurred because native ungulates in Yellowstone migrate seasonally and the intense, short-term grazing may provide plants sufficient recuperation time. The short time-frame of this experiment may have prevented plant recovery in part because under natural conditions rough fescue has a period of vegetative growth that lasts about 10 weeks (Stout et al. 1981), and most experiments that have measured plant recovery of rough fescue have lasted 8 to 16 weeks during the growing season (McLean and Wikeem 1985, Willms 1988, King et al. 1998).

Root morphological responses to clipping and fertilizer were not as great as I expected. A lack of root morphological response in this study may be a result of either high N availability or rapid nitrification of NH_4-N. Excess mineral N in the soil, particularly mobile NO_3-N, likely minimized importance of root biomass or morphology because N was not limiting. However, changes in root morphology as a result of nitrogen patches have included root proliferation (Jackson and Caldwell 1989, Pregetizer et al.

1993, Robinson et al. 1999), increased root branching (α-slope, Arredondo and Johnson 1999), and decreased root diameter (Jackson and Caldwell 1989). But these responses are not consistent across studies (Robinson et al. 1994). In addition, the adventitious root systems of grasses tend to be less sensitive to nutrient patches (Fitter and Stickland 1991, Taub and Goldberg 1996). In a 27-day pot experiment with perennial grasses, Fransen et al. (1999) found no difference in specific root length, branching frequency, or root length in response to nitrogen patches. Alternatively, recovery of ^{15}N-labelled fertilizer (per unit root biomass) increased in response to nutrient patches. As a result, they suggested physiological plasticity of roots was more important for nitrogen uptake than root morphology. Physiological changes have commonly been reported with clipping (Thornton and Millard 1997, Mackie-Dawson 1999, Paterson and Sim 2000), and are implicated in this study because N uptake per root biomass was greater under clipping. Changes in root physiology, versus morphology, may provide a more rapid response in nutrient uptake after defoliation that could be responsible for higher aboveground N (g) per root (g) in fescue plants. Alternatively, I did not measure mycorrhizal colonization of roots even though they can be abundant on rough fescue plants (McInenly, unpublished data), and could increase the belowground surface area necessary for nutrient uptake under limited root biomass (Marschener 1998).

Increased aboveground N (g) per root (g) with clipping could also be due to allocation of nitrogen from roots and crowns to shoots as documented by Ruess et al. (1988) and Hamilton et al. (1998), and this is supported by decreased root and crown N concentrations. Allocation of N to shoots may be an important strategy for reestablishing photosynthesis levels providing C resources that may eventually be utilized belowground to recoup root biomass (Paterson and Sim 2000).

While consistent application of either ammonium or nitrate did not affect root morphology, excess NO_3-N generally increased the risk of mortality and decreased the occurrence of root births, which may be why I observed a sharp decline in root hairs and root order after the first week of fertilization. In contrast to fertilizer type, clipping resulted in a decline in root hairs. Although this decline may have resulted from clipped plants producing fewer new roots (births), decreases in root order and average root diameter reflecting fewer small, new roots was not evident with clipping, and this was consistent field results (Chapter 3). Arredondo and Johnson (1998) found similar results with Whitmar, a grazing-sensitive cultivar of bluebunch wheatgrass (*Pseudoroegneria spicata*), which did not experience changes in root diameter with defoliation. They suggested grazing-tolerant species, as opposed to grazing-sensitive species, exhibit increased root diameter after defoliation because those plants may preferentially invest root carbon into coarse roots, instead of fine roots, resulting in longer life-spans and greater specific nutrient uptake rates.

Contrary to my hypothesis, application of NO_3-N did not improve the recovery of defoliated plants. Other studies have reported that plant and shoot biomass tend to decrease under NH_4-N only nutrition (Nowak et al. 1993, Walch-liu et al. 2001, Schortemeyer et al 1996, Abdelloui and Talouizte 2001, Hawkins and George 2001), and the negative effect has been attributed to decreased soil pH (Anderson et al. 1991, but see Griffith et al. 1997). However, higher total plant N, shoot N and root N uptake without a change in ^{15}N recovery under NH_4-N fertilization indicated that plants provided NH_4-N fertilizer were also using other sources of N. Plants may have used the N that was in soil prior to the fertilization treatment to a greater extent than plants provided NO_3-N. Ammonium-fertilized plants may have benefited from mixed nutrition because the initial soil nitrogen was primarily NO_3-N, whereas nitrate-fertilized plants had very little NH_4-N available for uptake. Further, my NH_4-N treatment is confounded because even though NH_4-N was supplied regularly, it was nitrified, because I did not use a nitrification inhibitor, and plant production has been shown to increase under NO_3-N nutrition (Stitt and Feil 1999, Bauer and Bernston 2001). Mixed N-source has been documented to enhance nitrogen uptake and tillering in wheat (Wang and Below 1992) and plant yield (Wiesler, 1997). And Bailey (1998) suggested that plants may absorb NH_4-N and NO_3-N at nearly equal rates in order to maximize the advantages and minimize the disadvantages of the two N-forms.

My results also reflect a high N-application (~300 kg/ha); nonetheless these levels are similar to levels of fertilization that plants would experience resulting from ungulate excreta (38 – 51 g N m^{-2}; Stillwell 1983, Day and Detling 1990, Seagle et al. 1992, Hamilton et al. 1998, Wilsey 2002, Peek and Forseth 2003). In a greenhouse experiment on *Agrostis capillaris*, Williams et al. (2003) found defoliation plus fertilization with simulated sheep urine (500 kg ha^{-1}) also decreased biomass whereas fertilization alone increased biomass. In grazed swards, urea from urine hydrolyses rapidly, resulting in a short-term flush of available NH_4-N that is not entirely consumed by plants and the remaining fraction is often nitrified (Williams et al. 2003).

Because total plant N uptake, and the % utilization of fertilizer, was lower with clipping, plant uptake was not likely responsible for lower soil NH_4-N under defoliated plants. Similarly, microbial immobilization of applied NH_4-N as a result of defoliation is not indicated because clipped plants had a lower recovery (%) of fertilizer N in soil organic N and there were no treatment effects on the amount soil organic N. Instead, I suggest nitrification of NH_4-N resulted in decreased ammonium under clipped plants. Greater soil moisture under clipped plants likely resulted from decreased demand from lower plant growth and warm, moist soil conditions can result in high nitrification of NH_4-N fertilizer (Bollman and Conrad 1998).

Unexpectedly, unclipped plants provided NH_4-N fertilizer had approximately twice as much ^{15}N in the organic N fraction of soil than any other treatment. I hypothesize this is because unclipped plants had more labile C in soil and NH_4-N fertilizer provided a preferred N source for microbes (Zak et al. 1990, Eviner and Chapin 1997, Kaye and Hart 1997, Lipson and Näsholm 2001), resulting in higher microbial activity. While soil organic N consists of both microbial and non-microbial fractions, the non-microbial fraction is a result of microbial activity (Haugen-Kozyra et al. 1993). Greater root biomass of unclipped plants, in addition to greater root mortality and root births, could have resulted in higher root turnover and more labile C in the soil via root exudation and death (Korsaeth et al. 2001, but see Hamilton and Frank 2001). In short-term ^{15}N experiments, microbes have out-competed plants for both NH_4-N and NO_3-N but demonstrated a preference for NH_4-N uptake (Kaye and Hart 1997), likely due to the energetic cost of NO_3-N uptake (Eviner and Chapin 1997).

In conclusion, a combination of NH_4-N and NO_3-N availability is commonly found in grazed systems, as urea and fecal material is mineralized and subsequently nitrified. Greater root survival and production (birth) under NH_4-N fertilization may have resulted from the lower energetic cost of NH_4-N assimilation, whereas C in roots of NO_3-N fertilized plants was taxed by both clipping and N uptake. However, clipping reduced root elongation and the proportion of roots with root hairs, effectively decreasing root surface area and spatial exploration of the soil, which is important for NH_4-N acquisition. Because this experiment was conducted under high N-availability, changes in root morphology in response to N acquisition may not have been pronounced. Yet similar conditions may be associated with rough fescue recovery after grazing at sites of high N-return throughout the season (e.g. urine patches) or preferred habitats (Chapter 2). However, high N-availability may be temporary and occur primarily when the system is carbon-limited (Holland and Detling 1990). Alternatively, microbial activity, represented in this study by high recovery of ^{15}N in the organic fraction of soils under NH_4-N fertilized plants that were not clipped, indicate potential competition between plants and microbes for N may exist.

Greater understanding of the influence of mineral N-form on rough fescue recuperation from defoliation would benefit from a similarly designed pot experiment that ensured prohibition of NH_4-N nitrification and where the microbial component of the soil was measured. In addition, monitoring root demography in the field in response to ^{15}N labeled urine applied seasonally and monitored over time would improve our ability to predict fescue response to grazing during different seasons. Further, this study has focused on nitrogen as a limiting factor, but field studies indicate phosphate loss rather than nitrogen may be of greater concern to the sustainability of fescue grasslands under heavy cattle grazing (Dormaar and Wilms 1998). Whether similar concerns exist under seasonal grazing by native herbivores is unknown.

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CHAPTER 5

SYNTHESIS

5.1 SUMMARY AND CONCLUSIONS

Herbivores have been widely implicated in the promotion of plant and nutrient heterogeneity, at various spatial scales, via urine and fecal deposition (Day and Detling 1990, Hobbs 1996, Frank and Evans 1997, Hamilton et al. 1998), visitation of preferred plants or locations such as vegetation edges (Senft et al. 1987, Wallace et al 1995, Hobbs 1996, Frank and Groffman 1998, Palmer and Hester 2000, Steinauer and Collins 2001), or migration across landscapes (McNaughton 1985, Archer and Smeins 1991, Frank et al. 1998, Augustine and Frank 2001). This study has documented effects of elk that likely increase plant and nitrogen heterogeneity at large and small scales.

At the landscape level, elk use at the Ya Ha Tinda Ranch grassland is spatially and temporally variable, with distribution related to forage abundance and, potentially, seasonal precipitation and predation. Elk distribution at the ranch results in a heterogeneous pattern of forage utilization which may allow the plant communities to remain in early- and late-successional states (Vavra and Ganskopp 1998). These spatial and temporal shifts may alter the composition of the rough fescue community via selection of preferred forage (WallisDeVries et al. 1999) and high urinary-N input (Olff and Ritchie 1998). In fact, high urine and fecal deposition on the eastern portion of the ranch provides a readily available source of mineral N, which could assist in the recuperation of plants responding to defoliation during the growing season. Greater N input in the eastern grasslands may be responsible for reported greater productivity (Benn et al. 1988) and fall standing biomass on that portion of the ranch. Forage biomass, as well as high nutrient content, influences ungulate foraging behavior (Wallace et al. 1995).

Ungulate herbivory may also affect plant diversity by changing the dominant plant species (Olff and Ritchie 1998), as was observed at the Ya Ha Tinda ranch. Defoliation later into the growing season decreased rough fescue and plant community diversity and increased more grazing-tolerant, but less palatable, species such as shrubs and sedges. However, defoliation removed standing dead and increased the relative amount of green biomass available to herbivores, and this effect was greater as defoliation continued into the growing season. Research suggests that removal of cured forage may increase the nutritional status of elk (Vavra and Ganskopp 1998) by improving the quality of available forage, as was observed in this study. However, a trade-off between dormant-season/early-spring grazing and year-round grazing occurs because while higher quality green plant material becomes more available under year-round defoliation, greater biomass and total shoot N result from defoliation that ceases earlier in the year. Grazer-induced increases in the availability of high quality food likely result in preferred foraging patches (Jeffries et al. 1994, Wallace et al. 1995), resulting in a positive feedback for both plants, from high nitrogen deposition, and for animals, from improved plant N.

At the patch level, urine deposition and subsequent N mineralization and nitrification may provide a combination of NH_4-N and NO_3-N, supplying rough fescue a mixed N-source from which grazed plants may benefit. Heterogeneity in soil nutrients may elevate the importance of plasticity in root morphology or physiology. At the plant-level, defoliation of rough fescue in the greenhouse experiment reduced root growth, effectively decreasing root surface area and spatial exploration of the soil, potentially increasing the value of mobile NO_3-N in the soil. However, NH_4-N in the soil is less energetically costly to assimilate, and may increase root survival and production (birth) when root carbon is at a premium. In addition, results from the greenhouse experiment indicate there is a potential for competition between plants and microbes for N when NH_4-N is provided, probably because NH_4-N is preferred over NO_3-N for microbial uptake.

In addition to spatial heterogeneity, the temporal nature of elk grazing at the Ya Ha Tinda, with higher use in the winter, will likely sustain the rough fescue grassland, as plants clipped in winter and spring had recovered by the end of the growing season at the majority of exclosure sites. However, changes in the migratory behavior of elk leading to grazing during the growing season at the ranch may threaten the sustainability of the rough fescue grassland, as aboveground standing biomass of fescue plants decreased under year-round clipping and, although not significant over the 2-year period of the field experiment, root biomass tended to decrease with defoliation in the growing season.

While elk distribution and grazing intensity on the Ya Ha Tinda was patchy, site variation appeared to have had a larger influence on plant response than 2-year clipping treatments (Milchunas and Lauenroth 1993, Verchot et al. 2002). For example, soil moisture had a much greater effect on belowground biomass and most nitrogen pools than clipping or natural grazing. Similar to findings in Yellowstone National Park (Verchot et al. 2002), soil properties were highly variable among exclosure sites and likely overrode most grazing effects.

In conclusion, elk grazing at the Ya Ha Tinda is patchy at the landscape-level and is influenced by both biotic and abiotic factors. Defoliation prior to the cessation of rough fescue vegetative growth, as would occur if elk migratory behavior were maintained, appears to maintain rough fescue while providing positive nutrient feedback via urinary and fecal deposition. Defoliation during the growing season decreased rough fescue root biomass, and this is a result of decreased root growth (elongation and births), not increased root mortality. Changes in the root morphology of rough fescue under grazing likely decrease the spatial exploration of the soil, unless mycorrhizal fungus can compensate; however, the influence of mineral N-form on nitrogen uptake is still unclear. Under high nitrogen availability, N mineralization and nitrification provide mineral N in forms that can potentially be exploited by rough fescue through different N-uptake strategies.

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Appendix I. All Candidate Models.

Structure	Parameters	Log likelihood	Wald Chi^2	df	*P*	AICc	ΔAICc
Summer							
Logistic	%Fescue, SSI, Chernozem, %Standing material, Topslope, Year, Dist to cov # Dk horse pg	-305.715	56.01	8	<0.001	627.70	0
Logistic	**%Fescue, %Standing material, Year # Dk horse pg**	**-315.745**	**53.34**	**4**	**<0.001**	**639.56**	**11.86**
Logistic	%Fescue, %Standing material # Dk horse pg	-318.779	48.54	3	<0.001	643.60	15.90
Logistic	%Fescue, # Dk horse pg	-339.755	15.21	2	<0.001	683.53	55.83
Logistic	%Standing material, # Dk horse pg	-322.224	44.86	2	<0.001	648.47	20.77
Logistic	%Fescue	-345.274	8.15	1	<0.00	692.56	64.85
Logistic	%Standing material	-327.106	41.24	1	<0.001	656.22	28.52
Logistic	# Dk horse pg	-344.491	5.80	1	<0.05	690.99	63.29
Logistic	Grassland, SSI, Chernozem, %Standing material, Topslope, Year, Dist to cov # Dk horse pg	-308.896	52.17	8	<0.001	634.07	6.36
Logistic	%Standing material, Year, # Dk horse pg	-319.308	51.37	3	<0.001	644.66	16.96
Poisson	%Fescue, SSI, Chernozem, %Standing material, Topslope, Year, Dist to cov # Dk horse pg	-501.959	57.55	8	<0.001	1020.2	392.5
Poisson	Grassland, SSI, Chernozem, %Standing material, Topslope, Year, Dist to cov # Dk horse	-508.935	48.19	8	<0.001	1034.1	406.4
Negative Binomial	%Fescue, SSI, Chernozem, %Standing material, Topslope, Year, Dist to cov # Dk horse pg	-464.045	55.77	8	<0.001	944.36	316.66
Negative Binomial	Grassland, SSI, Chernozem, %Standing material, Topslope, Year, Dist to cov # Dk horse pg	-467.749	50.42	3	<0.001	951.78	324.08
ZINB	%Fescue*, SSI*, Chernozem*, %Standing material*, Topslope*, Year*, Dist to cov*, # Dk horse pg*	-435.720	30.97	8	<0.001	940.51	312.81
Winter							
Negative Binomial	%Fescue, SSI, Chernozem, Easting, Topslope, Year, Dist to cov, Dkhor25	-1082.884	269.11	8	<0.001	2184.12	NA
Negative Binomial	%Fescue, SSI, Chernozem, Easting, Topslope, Year, Dist to cov	-1086.67	273.05	7	<0.001	2189.62	11.59
Negative Binomial	%Fescue, Chernozem, Easting, Topslope, Year, Dist to cov	-1096.31	252.63	6	<0.001	2206.84	28.81
Negative Binomial	%Fescue, Chernozem, Easting, Year, Dist to cov	-1105.93	230.50	5	<0.001	2224.03	46.00
Negative Binomial	Grassland, SSI, Chernozem, Easting, Topslope, Year, Dist to cov, # Dk horse pg	-1078.04	305.50	8	<0.001	2156.07	NA
Negative Binomial	Grassland, Chernozem, Easting, Topslope, Year, Dist to cov	-1092.30	300.52	6	<0.001	2184.60	6.57
ZINB	%Fescue *, SSI *, Chernozem*, Easting*, Topslope*, Year*, Dist to cov*, # Dk horse pg*	-1055.69	141.47	8	<0.0001	2144.45	NA
ZINB	%Fescue *, Chernozem, Easting*, Topslope, Year, Dist to cov	-1081.015	124.20	6	<0.0001	2178.31	0
ZINB	**%Fescue, Chernozem, Easting*, Topslope, Year, Dist to cov**	**-1082.74**	**142.25**	**6**	**<0.0001**	**2179.69**	**1.66**
ZINB	Grassland*, SSI *, Chernozem*, Easting*, Topslope*, Year*, Dist to cov*, # Dk horse pg*	-1052.67	174.59	8	<0.0001	2138.42	NA
ZINB	Grassland, Chernozem, Easting*, Topslope, Year	-1087.49	160.50	5	<0.0001	2189.19	11.16

Appendix II. Modified basal area calculations developed to be used in association with United States Forest Service measurement protocol (Cook et al. 1988).

Plant Shape	Basal area calculation
Circular	$\pi * (\text{radius})^2$
Elongated	$\pi * (((\text{length}*\text{width}/2)/2))^2$
Arced	$(\pi * ((\text{chord}/2)*(\text{width}/2))) - (\pi * (\text{chord-width}/2)^2)$
Ringed	$\pi * (\text{width})^2$